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Lake Ontario Long Term Biological Monitoring Program: Report for 1981 and 1982.

Ora E. Johannsson, R.M. Dermott,
R. Feldkamp, J.E. Moore

Great Lakes Fisheries Research Branch,
Canada Centre for Inland Waters,
867 Lakeshore Road, P.O. Box 5050,
Burlington, Ontario. L7R 4A6

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and Aquatic Sciences No. 1414

Lake Ontario

Long Term Biological Monitoring Program:

Report for 1981 and 1982

1985

by

Ora E. Johannsson
R. M. Dermott
R. Feldkamp
J. E. Moore
Department of Fisheries and Oceans
Great Lakes Fisheries Research Branch
867 Lakeshore Road
P.O. Box 5050
Burlington, Ontario L7R 4A6

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ABSTRACT

Johannsson, Ora E., R. M. Dermott, R. Feldkamp, and J. E. Moore, 1985. Lake Ontario Long Term Biological Monitoring Program: Report for 1981 and 1982. Can. Tech. Rep. Fish. Aquat. Sci. 1414. i-xvi + 208pp.

The Bioindex, or Long Term Biological Monitoring Program, was developed to: 1) determine normal seasonal patterns and annual ranges of abundance, community structure, and when possible, productivity of the biological components - phytoplankton, zooplankton, and benthos; 2) relate the biological components to variations in the physical, nutrient, and biological environment; and, 3) assess the adopted sampling strategy for long term monitoring.

The results from the first two years are presented and compared with historical data. Changes in abundance and community structure are compatible with the decreases in phosphorous loadings to the lake and continuing severe alewife predation. Seasonally weighted mean algal biomass in 1981, and 1982 was 50 percent lower than in 1970, while zooplankton abundance tripled. Benthic biomass fluctuated since the 1960s and indicate a slight decrease since 1968. Phytoplankton indicator species suggest a change from meso-eutrophic to meso-trophic/meso-oligotrophic conditions during this period.

It was concluded that the Bioindex sampling strategy is appropriate for long term monitoring. Improvements suggested include integrative sampling for all parameters, hypolimnetic zooplankton sampling and net calibration studies.

RESUME

Johannsson, Ora E., R. M. Dermott, R. Feldkamp, and J. E. Moore, 1985. Lake Ontario Long Term Biological Monitoring Program: Report for 1981 and 1982. Can. Tech. Rep. Fish. Aquat. Sci. 1414. i-xvi + 208pp.

Le Bioindex, ou programme de surveillance biologique à longue date, a trois objectifs principaux: 1) déterminer les tendances saisonnières normales et les variations annuelles de la quantité, de la structure des communautés et, si c'est possible, de la productivité des composants biologiques (phytoplancto , zooplancton et benthos); 2) établir la relation entre les composants biologiques et les variations de l'environnement physique, biologique et chemique; 3) évaluer la valeur de la méthode d'échantillonnage utilisée pour la surveillance à long terme.

Les résultats des deux premières années d'étude sont présentés ici et comparés avec des données chronologiques. Les changements dans la quantité et la structure des colonies semblent aller de pair avec les diminutions de charges de phosphore dans le lac et la prédation intense et continuelle du gaspareau. La moyenne pondérée sur les saisons de la biomasse des algues a baissé de 50 p. 100 en 1981 et 1982 par rapport à 1970, alors que la quantité de zooplancton a triplé. La biomasse benthique a varié depuis les années 1960 et manifeste une légère diminution depuis 1968. Les données récoltées sur les espèces de phytoplancton utilisées comme indicateur suggèrent que les conditions du lac sont passées de méso-eutropes à mésotrophes ou méso-oligotrophes au cours de cette période.

On a conclu que la méthode d'échantillonnage Bioindex était appropriée à la surveillance à long terme. Pour l'améliorer, on suggère d'intégrer un échantillonnage pour tous les paramètres, d'échantilloner le zooplancton hypolimnique et d'effectuer des études d'étalonnage net.

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INTRODUCTION

The Bioindex, or Long Term Biological Monitoring Program, is a preliminary or developmental program for biological monitoring on Lake Ontario. The attempt to conduct more intensive biological monitoring was prompted by the International Joint Commission's acceptance in 1978 of a broader definition of lake health encompassing all components of the ecosystem. Many of man's activities such as fishing, nutrient loading of lakes and rivers, shoreline alteration, and contaminant production, ultimately affect the lake ecosystem. The effects of these stresses are not always known and cannot be monitored individually. Biological monitoring is an integrative monitoring strategy. Ecosystems respond to stress with compensatory changes in community structure and function mediated at the population level (Boesch and Rosenburg, 1981). Therefore, changes in ecosystem health (or state) can be detected by monitoring changes in the biotic communities (Nicholls et al., 1980; Dillon et al., 1978).

Any monitoring program must first document the state of the ecosystem, namely, the species composition, biomass, and production of each community component, including the normal ranges of temporal and annual variation. The second step is to examine the relationships and interactions amongst the ecosystem components in order to interpret and predict future changes in community structure or function. Thus, the value of such a monitoring program goes far beyond its surveillance capabilities; it can form the backbone for research activities, thereby encouraging a detailed understanding of the system.

The design of the Bioindex Program was developed jointly by many people at the Canada Centre for Inland Waters, but particularly by the scientists in the Great Lakes Fisheries Research Branch of the Department of Fisheries and Oceans: Dr. C. K. Minns, Dr. J. Cooley, Dr. N. Watson and Dr. H. Shear. The present report is an introduction to and assessment of the Bioindex Program. The analyses of the first two years of data, 1981 and 1982, were designed to establish the state of the Lake Ontario ecosystem, and to investigate the type of sampling strategy best suited for the long-term surveillance of the lake. The methods and frequency of sampling and the influence of station location were examined. The state of the ecosystem was defined seasonally. An attempt was made to organize the seasonal pattern in a manner which was mathematically comparable between years, and to investigate the degree of variability observed between years and amongst stations. In addition, the 1981 and 1982 communities were compared with earlier observations.

METHODS

STATION SELECTION

Four Bioindex sampling stations were selected to represent distinct regions or influences within the open water area of Lake Ontario based on the earlier work of Patalas (1969), Munawar and Nauwerck (1971), Stadelmann et al. (1974), and El-Shaarawi and Kwiatkowski (1977). Station 41 is located in the more stable, less productive, mid-lake region; station 12, is in the area of upwelling events on the north shore of the western basin; station 81 is in the more productive eastern basin; station 93 is within the influence of the Niagara River, the single largest source (84 percent) to the lake

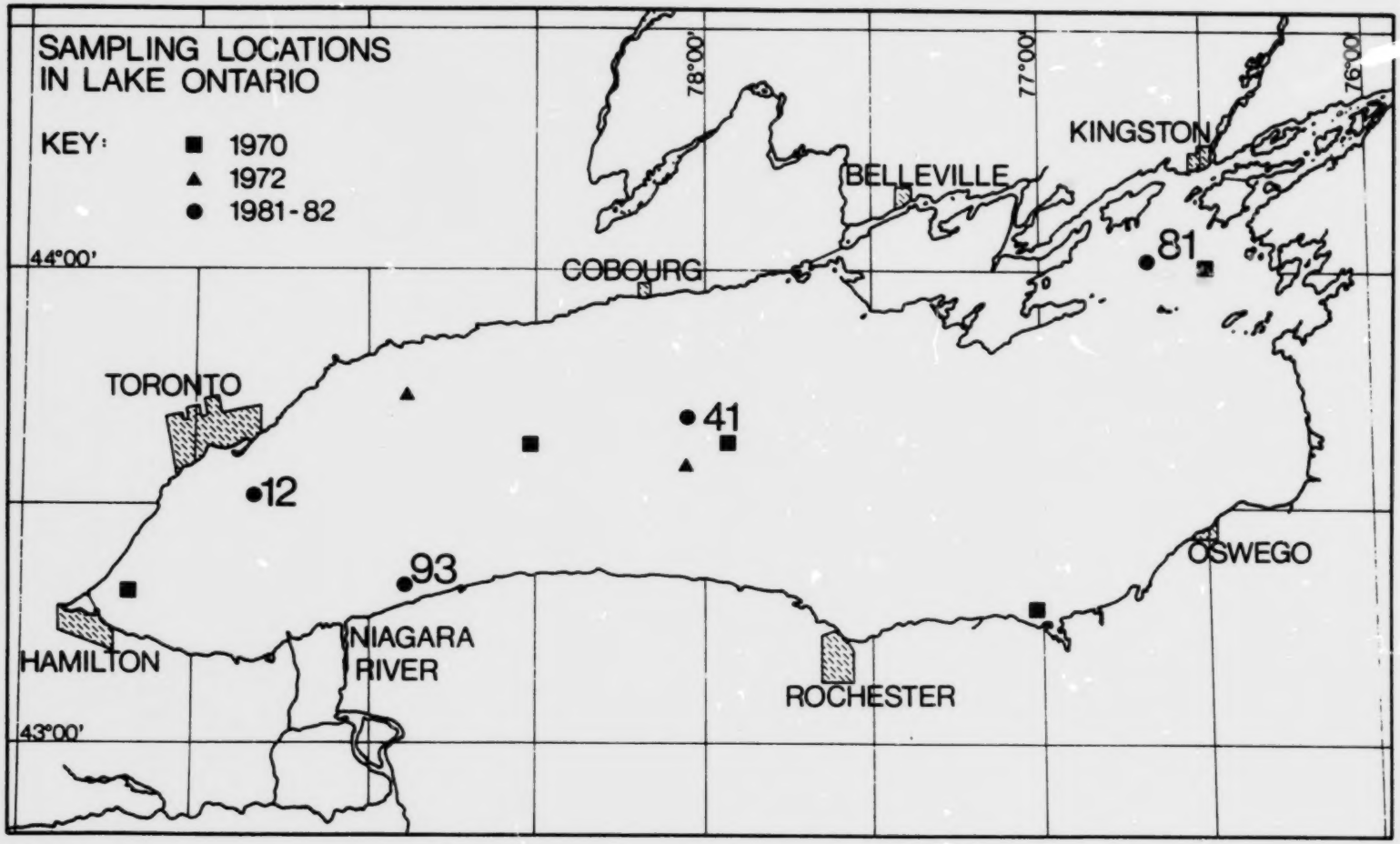


Figure 1. Lake Ontario, showing the location of the four Bioindex stations: 12, 41, 81 and 93. The 1970 and 1972 sites are mentioned in the text.

(Fig. 1). In order to maximize the continuity of data in the Federal Government data base on Lake Ontario, the exact locations were chosen to coincide with permanent, long-term surveillance stations.

SAMPLING PROGRAM

During the 1970s the Inland Waters Directorate (IWD) conducted several spatially-intensive, seasonal (monthly) surveys of Lake Ontario for physical, chemical, and biological parameters. The biological parameters measured were particulate organic carbon (POC), particulate organic nitrogen (PON), and chlorophyll a (CHLA). The results of these surveys indicated that there was much more variability in the temporal than in the spatial data (El-Shaarawi and Kwiatkowski, 1977). Minns (1984) obtained a similar result with zooplankton data. Consequently, the Bioindex Program was formulated to study a few sites in detail. Samples were collected weekly from mid-March until the end of November. Table 1 presents an overview of the sampling regime, and indicates the parameters measured, the sampling depths, and the type of samples collected. All physical and chemical parameter measurements were obtained from discrete depth samples, while zooplankton and phytoplankton were collected with integrating samplers. Chemical biomass indicators such as POC, PON and CHLA were measured in both discrete and integrated samples.

All samples were collected in duplicate. The filtering and sample preparations were completed on board ship and the chemical analyses were performed later by the Great Lakes Water Quality Laboratory (IWD). In May 1982, GF/C filters used to measure chlorophyll concentrations were replaced by the more efficient Millipore filters (Munawar et al., 1982). The analyses were then conducted by personnel of the Great Lakes Fisheries Research

TABLE 1: Bioindex sampling regime at stations 12, 41, 81 and 93 in 1981 and 1982. Group A parameters were measured from integrated water samples. Group B parameters were taken with a rosette sampler at discrete depths. Note that stations 81 and 93 were too shallow to take the full complement of samples.

	Sampling Depth(m)	Number of Samples			
Stations		12	41	81	93
Sounding Depths		110m	128m	37m	17-20m
Isothermal Conditions					
Discrete Depth Samples	1	2	2	2	2
	10	2	2	2	2
	25	2	2	-	-
	Bottom - 10	2	2	2	-
	Bottom - 2	2	2	2	2
Integrated Samples	0 to 20	2	2	2	2
Stratified Conditions					
Discrete Depth Samples	1	2	2	2	2
	1 m above thermocline	2	2	2	2
	1 m below thermocline	2	2	2	2
	Bottom - 10	2	2	-	-
	Bottom - 2	2	2	2	-
Integrated Samples	0 to 1 m above thermocline or 0 to 20 m whichever was less	2	2	2	2

Group A: Phytoplankton, Zooplankton, Chla, POC, PON, Ash W, Dry W.
Group B: pH;, Alka, Cond, TP, TFP, SRP, TKJN, PON, NH_3, NO_3NO_2, Cl, SRS, Chla, POC.

Branch. Zooplankton were identified and enumerated by Dr. W. T. Geiling, phytoplankton by Mr. D. Beliveau, and benthos by Dr. S. Kakonge.

The following is a list of the parameters studied with their methods of measurement. All chemical determinations are described in much greater detail in Philbert and Traversy (1973) or Inland Waters Directorate (1979).

A) Physical Parameters

Temperature: (EBT) a temperature profile from surface to bottom was obtained with an electronic bathythermograph (°C).

Sounding Depth: The water depth was determined acoustically with an echo sounder. (m)

Dissolved Oxygen: ($DISSO_2$) The oxygen concentration of the water was determined by Winkler titration using the modified Winkler iodometric measure. ($gO_2.m^{-3}$)

Euphotic Depth: (EU) a vertical profile of horizontal transparency was obtained with a transmissometer using a 0.25 m pathlength (CSS Bayfield) or a 1 m pathlength (CSS Limnos) and Wratten 45 blue-green filters. The following relationships, developed by Dr. J. Jerome (National Water Research Institute, Burlington, Ontario, pers. comm.), were used to calculate beam and light attenuation:

Beam attenuation (C) = $\text{Ln} \left(\frac{100}{T}\right)^{1/P}$ where: T = transmission reading
P = pathlength

To convert $C_{1.0}$ to $C_{.25}$:

TRANS >30% $C_{.25} = 0.882 * C_{1.0} - 0.431$

TRANS <30% $C_{.25} = 0.984 * C_{1.0} - 0.947$

Light Attenuation (K) = $0.185 * C_{.25} + 0.02$

The depth of one percent light penetration was then calculated from the following equation:

$EU = \frac{\ln(Io) - \ln x\ (Ieu)}{K}$ where: Io = 100% subsurface radiation

Ieu = % radiation at depth EU (1%)

Secchi Disc Depth: (SECCHI) The vertical transparency was measured as the depth of disappearance of a 30 cm diameter white disc. (m)

Conductivity: (COND) Specific conductance was measured with a conductivity meter at ambient temperature and converted to 25°C. ($\mu mhos.cm^{-1}$)

pH: (pH) Measurements were made with a radiometer model pH52 digital readout pH meter.

Alkalinity: (ALKA) The sample was filtered through a GF/C filter, mixed with HCl, and then mixed with oxygen. The resulting CO_2 was separated from the liquid phase and measured with an infrared detector. ($gCaCO_3.m^{-3}$)

Chloride: (CL) The chloride concentrations of filtered samples (0.45 μ membrane filters) were determined using the autoanalyzer mercuric thiocyanate method. ($gCl.m^{-3}$)

B) Nutrient Parameters

Total Phosphorus: (TP) A 110 ml water sample was preserved with 1 ml of 30% H_2SO_4 and later digested in acid persulfate. The phosphorous concentration was determined colorimetrically using the ammonium molybdate-stannous chloride method. ($gP.m^{-3}$)

Soluble Reactive Phosphorus: (SRP) A 110 ml sample was filtered through a 0.45 μ membrane filter and stored at 5°C. On return to the laboratory it was analyzed in the autoanalyzer using the ammonium molybdate-stannous chloride method. ($gP.m^{-3}$)

Total Filtered Phosphorus: (TFP) A 110 ml water sample was filtered through a 0.45 μ membrane filter, preserved with 1 ml of 30% H_2SO_4, and analyzed as per TP. ($gP.m^{-3}$)

Total Kjeldahl Nitrogen: (TKJN) A 110 ml water sample was filtered through a 0.45 μ membrane filter. The filtrate was digested with H_2SO_4 and an oxidant at 300°C in an autoanalyzer system. The concentration of the resultant $(NHK_4)_2SO_4$ was determined colorimetrically using salicylate and dichloroisocyanurate. ($gN.m^{-3}$)

Ammonia: (NH_3) A 110 ml sample was filtered through a 0.45 μ membrane filter and the N content determined by an automated alkaline phenol method. ($gN.m^{-3}$)

Nitrate Nitrite: (NO3NO2) The sample was filtered through a 0.45 μ membrane filter and the N content determined by the autoanalyzer cadmium reduction method. ($gN.m^{-3}$)

Soluble Reactive Silica: (SRS) The sample was filtered through a 0.45 μ membrane filter and the Si concentration determined by the autoanalyzer heteropoly-blue method. ($gSiO_2.m^{-3}$)

C) Biological Parameters

Dissolved Organic Carbon: (DOC) The concentration of DOC in a GF/C-filtered sample was determined by an automated ultraviolet method. ($gC.m^{-3}$)

Particulate Organic Carbon: (POC) The sample was filtered through a precombusted (500°C) GF/C filter. The carbon residue on the filter was analyzed using a Hewlett-Packard model 185 CHN Analyzer. ($gC.m^{-3}$)

Particulate Organic Nitrogen: (PON) The particulate nitrogen concentration was determined on the same filter, using the same equipment as the POC. ($gN.m^{-3}$)

Seston Dry Weight: (SDW) Dry weight was determined for integrated epilimnetic samples. The particulate matter retained by a precombusted (500°C) GF/C filter was dried to constant weight at 105°C. ($g.m^{-3}$)

Suspended Inorganic Matter: (SIM) The filter in the above analysis (SDW) was combusted at 550°C, cooled and weighed. The SIM was calculated from the difference. ($g.m^{-3}$)

Chlorophyll a Uncorrected (CHLAU): Two methods were employed. From March 1981 until May, 1982, the GF/C filtration/acetone extraction method described by Strickland and Parsons (1968) was used. After that date the samples were filtered through 0.45 μ Millipore filters which required the acetone extraction period to be extended to 17 h. ($mg.m^{-3}$)

Chlorophyll a Corrected (CHLAC): The phaeophytin concentration was determined by acidification of the above sample (Strickland and Parsons, 1968), and the CHLAC concentration determined by difference (CHLAU-phaeophytins). ($mg.m^{-3}$)

Phytoplankton: Integrated 250 ml whole-water samples were preserved with Lugol's solution, and the phytoplankton identified and enumerated using the Utermöhl inverted microscope technique (Utermöhl 1958, in Munawar *et al.*, 1974). A 15 ml aliquot was settled and examined using light/dark illumination and a Prior 29331 microscope fitted with Wild optics and condenser. At least 200 units/sample

were counted at 300 x, 600 x, and 1500 x magnification by the strip method providing an estimate of total cell numbers within ± 14 percent (Lund et al., 1958), and cell measurements taken. Phytoplankton volumes were calculated using approximations to geometric shapes, and converted to biomass assuming a density of one. The standard deviation of the total biomass of replicate hauls was ± 22.8 percent in 1982 (N=33 pairs) and ± 15.8 percent in 1981 (N=17 pairs). The most commonly used taxonomic references were Anton and Duthie (1981), Haworth (1981), Hustedt (1930), Findlay and Kling (1979), Lind and Brook (1980), Nygaard (1977), Patrick and Reimer (1966, 1975), Prescott (1970), Prescott et al., (1975), Schoeman and Archibald (1976-1979), Smith (1950), Taft and Taft (1971) and Webber (1971).

Zooplankton: Samples were collected with a 30 cm diameter 70 μ nitex mesh net. This net was lost in September, 1982 and replaced by a 25 cm diameter 64 μ mesh net for the remainder of the year. The net was lowered to the same depth as the phytoplankton samples, and hauled vertically through the water column at 0.5 $m.sec^{-1}$. The zooplankton were preserved in four percent sugared formaldehyde, and identified under a dissecting microscope using a stratified counting system (Cooley et al., 1986). The adult calanoids and cyclopoids, and the cladocera were identified, and the number of individuals and eggs/species recorded. The calanoid and cyclopoid nauplii and copepodites were counted, but not identified to species.

Benthos: During 1981 and 1982 three stations were sampled monthly: stations 81, 93a (Niagara - 70 m), and 41. During 1983, samples were only collected during April, July, and November. Stations 12 and 93 were also included. Five Ponar grab samples were collected each date and sieved using a 250 µ screen. Samples collected during April, July, and November were examined to enumerate all species present, and determine their dry biomasses. Pontoporeia sp. was enumerated in all samples and sorted into 1 mm size classes. The average length of each 1 mm size class of Pontoporeia sp. was measured, and length-weight relationships calculated for each station. Enumeration also included the number of gravid females present, numbers of eggs per female, and number of young present each month.

Using the mean lengths, growth rates of the young of the year were calculated. From the monthly numbers and weights of each size class, the biomass (standing stock) at each station was calculated as well as the total production of the populations based on the size frequency method (Krueger and Martin, 1980).

The respiration rates of different-sized Pontoporeia sp. were measured in laboratory experiments. Populations from each station were maintained in their native sediments at 5 and 10°C for several weeks. Respiration was measured using the micro-Winkler technique and was related to animal size and temperature.

DATA ANALYSIS

All chemical and physical measurements, taken at discrete depths within the epilimnion, were converted to integrated epilimnetic values so that they could be related to the integrated POC, PON, CHLA, phytoplankton and zooplankton data. A linear gradient was assumed between the discrete depth samples.

In the higher latitudes, temperature and light control the seasonal cycle of freshwater systems. Therefore, the chemical data and, for some analyses, the phytoplankton data were summarized by dividing the year into five seasonal-thermal periods and collating the information within each. Unless stated otherwise, the chemical concentrations discussed in the text refer to the mean concentrations observed within these periods. The separation between thermal periods coincided with natural breaks in the seasonal thermal pattern. The first period (0.0 - 5.9°C) coincided with cold, isothermal conditions during early spring. The second period (6.0 - 16.9°C) was a time of rapid warming and creation of the thermocline. The third period (>17.0°C) commenced with the formation of a distinct shallow epilimnion (<12 m) and continued as the epilimnion deepened in the autumn to 20 to 30 m. The fourth period (16.9 - 8.0°C) spanned the continuing erosion of the epilimnion and included the return to isothermal conditions in the nearshore areas. Period five (7.9 - 0.0°C) was a return to winter conditions.

Much of the data in this report concerns seasonal trends. When trends are graphed, missing data are ignored and the lines on the figures are continuous, being the best estimate available of temporal trends.

SECTION ONE: CHEMICAL AND PHYSICAL PARAMETERS

In this section the state of the Lake Ontario ecosystem is described in terms of seasonal trends and ranges. Analysis of variance techniques are applied to the seasonally grouped data to test the significance of inter-station and annual variability. In the second part of this section the relationships amongst the biological and environmental factors are investigated and sampling strategy is examined.

RESULTS

Technical difficulties invalidated the 1981 pH and COND data, and changes in the method of chlorophyll a analysis in May 1982 invalidated annual and 1982 seasonal chlorophyll a comparisons. Soluble reactive phosphorus was measured infrequently in 1981. For these reasons only the 1981 chlorophyll a and 1982 SRP, COND, and pH data were analyzed.

SEASONAL RELATIONSHIPS

Physical Regime

The physical regime is described in terms of seasonal patterns in thermal structure, light penetration, oxygen concentrations, pH, conductivity, alkalinity, and chloride. The mid-lake stations, 12 and 41 with sounding depths of 100 and 125 m respectively, are presented separately from the nearshore stations, 81 and 93, as physical conditions in these two regions differed significantly.

The mid-lake stations follow the classic description of thermocline development and erosion. The water is isothermal in March and warms slowly to 3° to 4°C by early to mid-June. Rapid warming then occurs and a distinct shallow epilimnion is formed. This may be the result of warmer nearshore water moving into the mid-lake region (Scavia and Bennett 1980). Events at station 12 precede those at 41 by approximately one week and initial epilimnion temperatures can be slightly lower, 7 to 12°C versus 12°C. Temperatures peak in July at or slightly above 20°C. The thermocline starts to deepen in August, and epilimnetic temperatures fall during September and October reaching approximately 9°C at turnover in October or November (Figs. 2a and 2b).

In spring the oxygen concentration of the water is near 13.8 $g.m^{-3}$, and decreases in mid-summer to 9.1 to 10.3 $g.m^{-3}$ when temperatures reach their highest. However, in terms of percent saturation, the levels of oxygen rise from 100 percent in the first thermal period to 122 to 132 percent in the second and third periods, and return to 100 percent in the fourth and fifth periods (Table 2).

The seasonal pattern in euphotic depth was constant from year to year although the actual depths varied. Light penetration was greatest in the spring ranging from 32 m in 1981 to 42 m in 1982 (cf. Table 3); the ratio of the euphotic depth to mixed depth (DZ/DM) was 0.3 to 0.4. As the season progressed light penetration decreased, reaching a minimum in period two or three. Summer (period three) levels in 1981 were 10 m while in 1982 they were 16 to 18 m. During periods two and three light penetrated into the thermocline and DZ/DM was normally 1.5 to 1.9 but reached 3.7 in 1982. The euphotic depth deepened again slowly through the autumn with fifth period values of 21 to 38 m and DZ/DM ratios of 0.2 to 0.4.

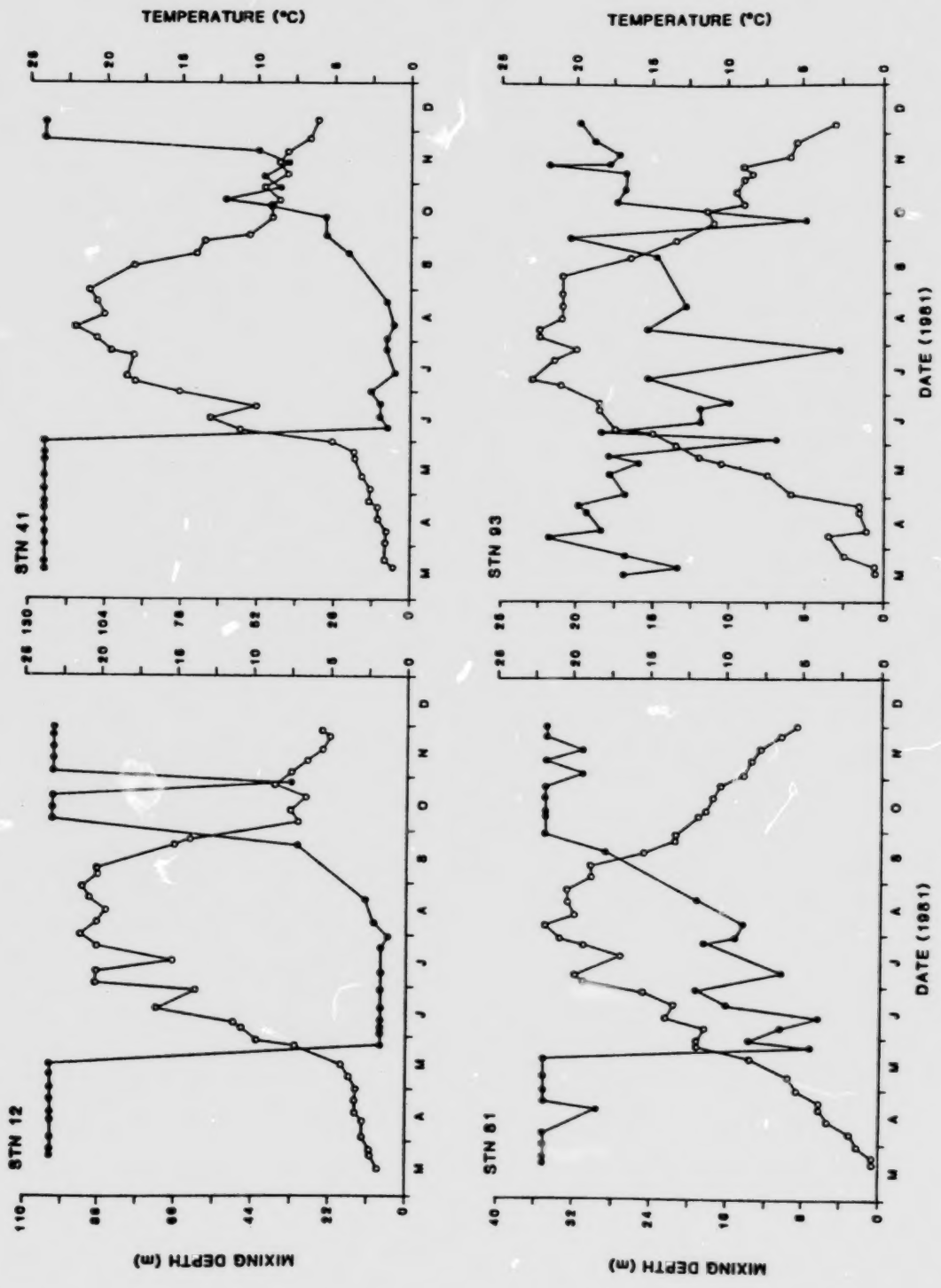


Figure 2a. Seasonal epilimnetic temperature (o) and mixed depth (●) regimes at the four Bioindex stations in 1981 and 1982. The mixed depth was defined from changes in the density gradients determined from the EBT traces.

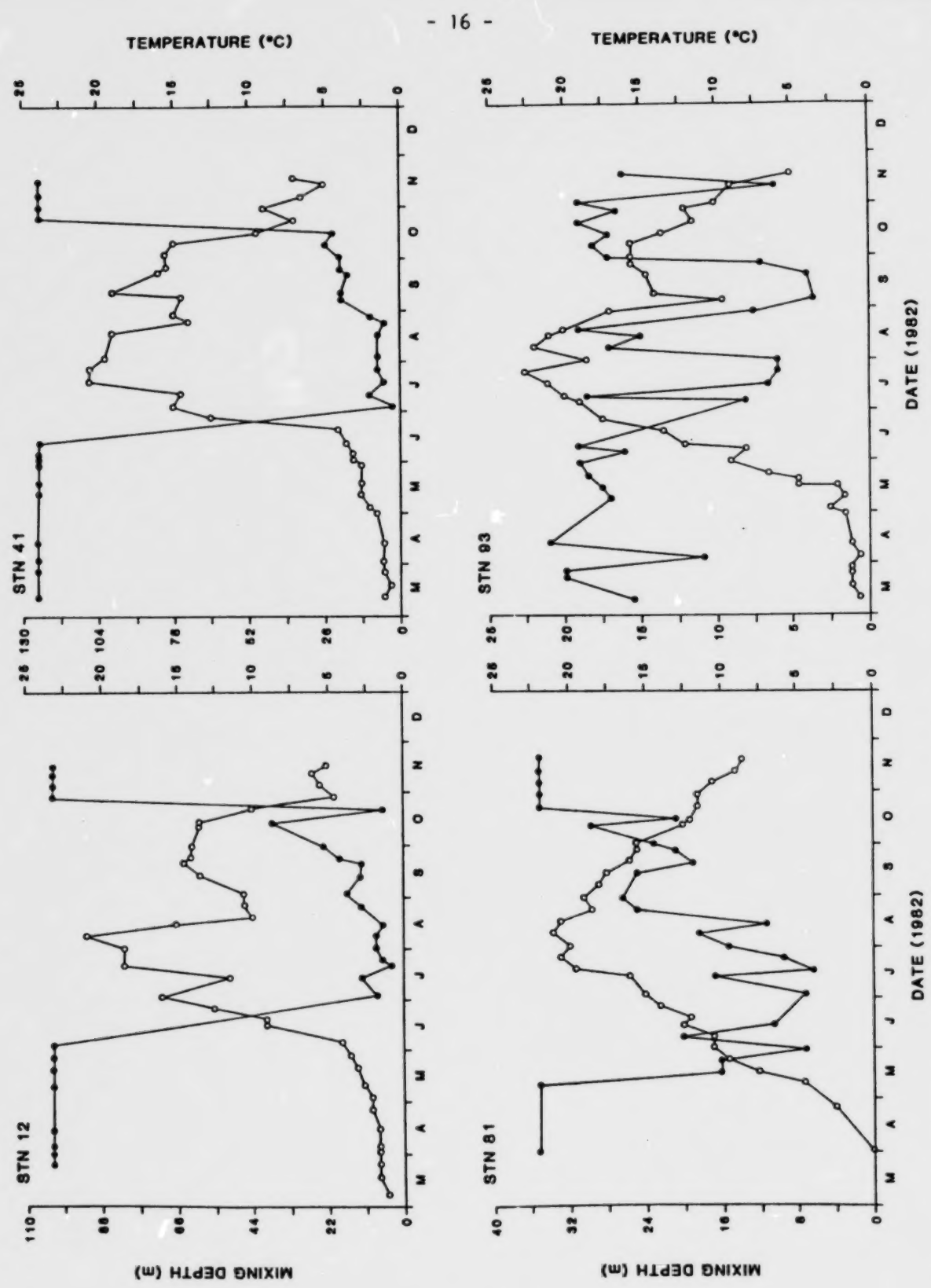


Figure 2a. Continued

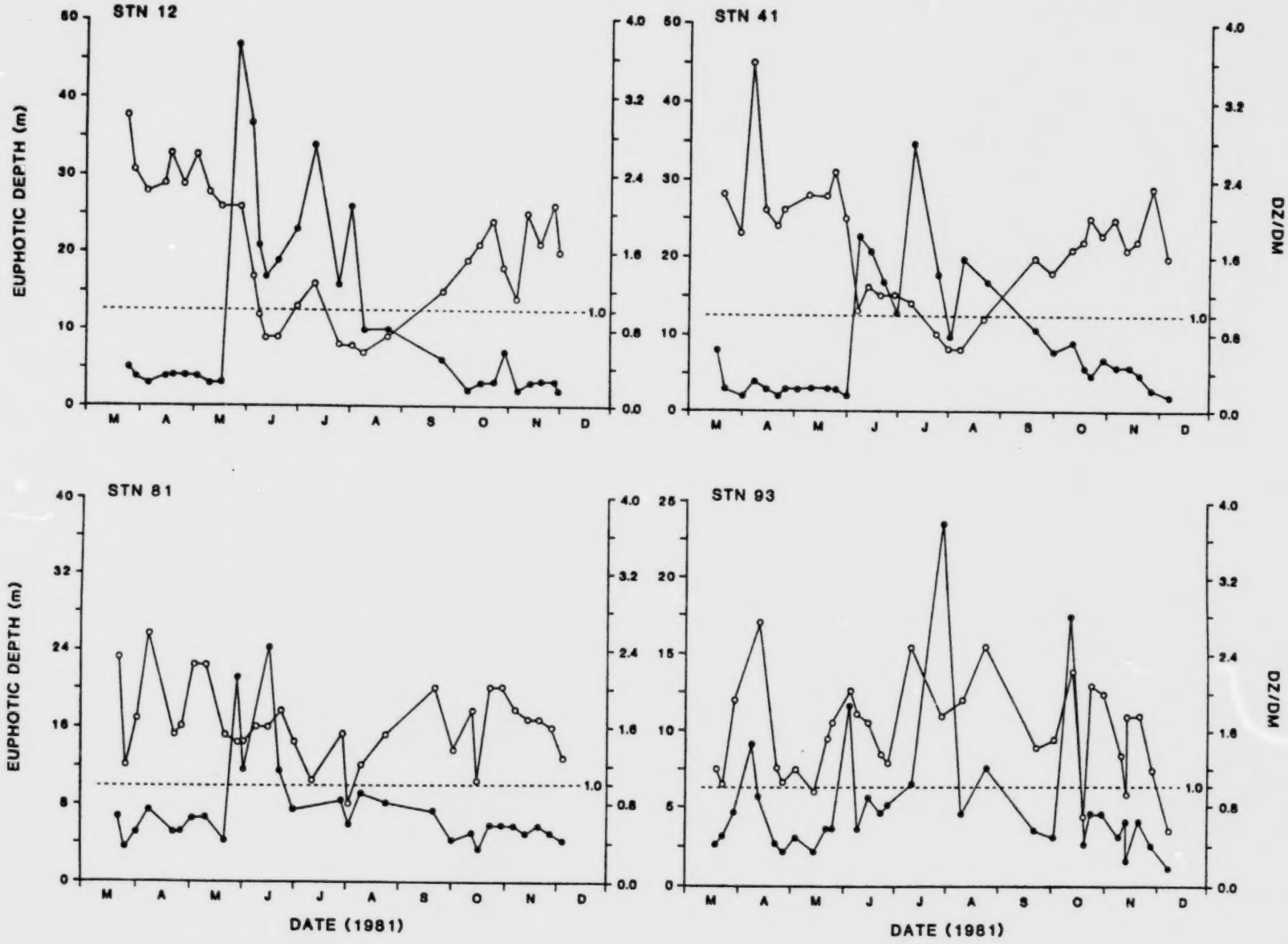


Figure 2b. Seasonal euphotic depth (o) and ratio of mixed depth to euphotic depth (o) regimes at the four Bioindex stations in 1981 and 1982.

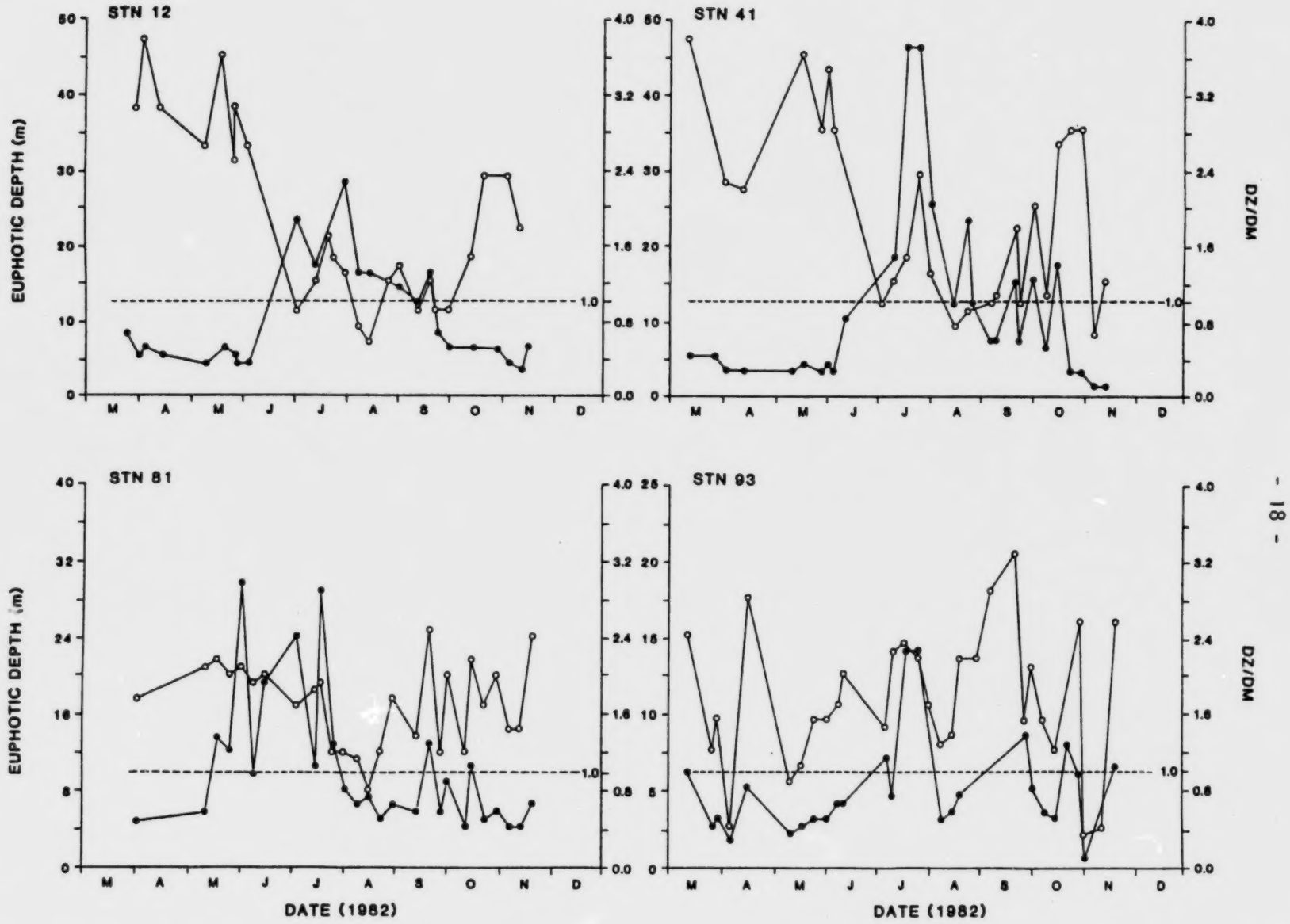


Figure 2b. Continued

TABLE 2: Oxygen percent saturation in the epilimnion.

Seasonal Period / Station	Year	Percent Saturation I	II	III	IV	V
12	1981	104	132	125	100	100
	1982	103	130	125	110	100
41	1981	105	125	120	103	99
	1982	103	130	122	110	102
81	1981	106	114	110	100	98
	1982	108	117	108	100	-
93	1981	105	116	112	105	100
	1982	108	113	115	105	-

TABLE 3a: Physical variables. Concentrations within the five seasonal thermal periods. Station 12, 1981.

Seasonal Thermal Period	EBT °C	ALKA G.M^{-3}	DISSO2 G.M^{-3}	CL G.M^{-3}	MIXED DEPTH M	EUPHOTIC DEPTH M	RATIO DZ/DM M
1							
MEAN	2.50	95.45	13.73	26.99	102.00	31.01	.30
STDEV	.57	2.51	.14	.44	0	3.32	.03
VALIDN	9	9	9	9	9	8	8
2							
MEAN	10.12	90.81	14.15	26.99	20.21	15.97	1.90
STDEV	3.99	4.54	.58	.26	36.07	7.47	1.13
VALIDN	7	7	7	7	7	7	7
3							
MEAN	19.77	84.87	11.36	26.60	8.82	11.80	1.89
STDEV	1.66	2.78	1.20	.82	4.98	4.10	1.71
VALIDN	11	11	11	11	11	11	11
4							
MEAN	9.83	93.44	11.19	26.70	66.00	18.74	.36
STDEV	3.76	2.53	.80	.33	39.50	3.23	.19
VALIDN	6	6	6	6	6	6	6
5							
MEAN	6.01	94.14	12.04	26.89	102.00	21.14	.21
STDEV	1.05	.77	.15	.22	0	4.95	.05
VALIDN	5	5	5	5	5	5	5
SEASONALLY WEIGHTED MEAN	10.7	90.9	12.4	26.8	30.1	18.8	0.96

TABLE 3a: Physical variables. Concentrations within the five seasonal thermal periods. Station 41, 1981.

Seasonal Thermal Period		EBT °C	ALKA G.M^{-3}	DISSO2 G.M^{-3}	CL G.M^{-3}	MIXED DEPTH M	EUPHOTIC DEPTH M	RATIO DZ/DM M
1								
	MEAN	2.58	95.34	13.90	26.82	126.00	28.36	.23
	STDEV	1.12	2.25	.30	.51	0	6.00	.05
	VALION	12	12	12	12	12	11	11
2								
	MEAN	12.33	91.75	12.36	26.96	10.38	14.40	1.46
	STDEV	2.37	2.60	.39	.23	2.93	1.25	.35
	VALION	4	4	4	4	4	4	4
3								
	MEAN	19.54	84.53	10.68	25.78	7.50	11.28	1.61
	STDEV	1.40	2.58	1.11	2.77	2.37	2.64	.55
	VALION	10	10	10	10	10	10	10
4								
	MEAN	10.14	92.48	11.08	25.73	39.36	21.37	.59
	STDEV	2.19	1.82	.55	2.61	13.18	2.40	.16
	VALION	9	9	9	9	9	9	9
5								
	MEAN	6.78	91.80	11.72	27.15	101.50	23.73	.26
	STDEV	.95	1.06	.26	.57	42.44	4.86	.11
	VALION	3	3	3	3	3	3	3
SEASONALLY WEIGHTED MEAN		10.6	90.8	12.0	26.2	57.8	21.2	0.85

TABLE 3a: Physical variables. Concentrations within the five seasonal thermal periods. Station 81, 1981.

Seasonal Thermal Period		EBT °C	ALKA G.M^{-3}	DISSO2 G.M^{-3}	CL G.M^{-3}	MIXED DEPTH M	EUPHOTIC DEPTH M	RATIO DZ/DM M
	1							
MEAN		2.69	93.33	14.31	25.88	34.31	18.27	.53
STDEV		1.86	1.78	.82	.78	1.94	4.64	.13
VALION		8	8	8	8	8	8	8
	2							
MEAN		11.67	93.74	11.95	25.86	17.74	16.26	1.26
STDEV		3.02	1.91	.62	.58	11.45	2.79	.71
VALION		8	8	8	8	8	8	8
	3							
MEAN		19.83	84.86	9.72	25.44	14.95	13.37	1.01
STDEV		1.29	2.08	.96	2.31	5.62	3.80	.47
VALION		11	11	11	11	11	11	11
	4							
MEAN		11.71	92.22	10.50	25.50	32.94	16.88	.52
STDEV		2.20	1.03	.55	1.85	3.24	3.08	.12
VALION		9	9	9	9	9	9	9
	5							
MEAN		6.63	92.05	11.73	26.70	33.67	15.33	.46
STDEV		1.06	.93	.19	.17	2.31	2.04	.09
VALION		3	3	3	3	3	3	3
SEASONALLY WEIGHTED MEAN		12.1	91.1	11.3	25.7	24.8	15.6	0.77

TABLE 3a: Physical variables. Concentrations within the five seasonal thermal periods. Station 93, 1981.

Seasonal Thermal Period	EBT °C	ALKA G.M^{-3}	DISSO2 G.M^{-3}	CL G.M^{-3}	MIXED DEPTH M	EUPHOTIC DEPTH M	RATIO DZ/DM M
1							
MEAN	1.64	94.42	14.46	22.07	18.24	12.56	.67
STDEV	1.22	4.91	.42	3.87	2.74	9.22	.40
VALIDN	7	7	7	7	7	7	7
2							
MEAN	11.82	90.71	12.18	20.34	15.23	9.63	.75
STDEV	4.13	2.37	1.20	1.67	4.21	2.15	.51
VALIDN	7	7	7	7	7	7	7
3							
MEAN	20.58	89.87	9.80	21.54	12.65	12.41	1.22
STDEV	1.88	2.63	.64	2.23	4.40	2.85	.89
VALIDN	13	13	13	13	13	13	13
4							
MEAN	10.32	96.18	11.27	21.76	15.14	10.57	.91
STDEV	1.66	1.37	.59	2.88	5.31	3.25	.85
VALIDN	7	7	7	7	7	7	7
5							
MEAN	4.89	95.36	12.48	23.74	18.83	7.23	.39
STDEV	1.69	.60	.56	1.43	1.26	3.60	.22
VALIDN	3	3	3	3	3	3	3
SEASONALLY WEIGHTED MEAN	12.7	92.3	11.5	21.7	14.6	10.9	0.95

TABLE 3a: Physical variables. Concentrations within the five seasonal thermal periods. Station 12, 1982.

Seasonal Thermal Period	EBT °C	ALKA $G.M^{-3}$	COND UMHOS	pH	DISSO2 $G.M^{-3}$	CL $G.M^{-3}$	MIXED DEPTH M	EUPHOTIC DEPTH M	RATIO DZ/DM M
1									
MEAN	2.14	94.91	313.28	7.76	13.73	26.81	102.00	37.20	.36
STDEV	.95	2.92	19.07	.41	.25	.43	0	5.02	.05
VALID	13	13	13	11	13	13	13	8	8
2									
MEAN	11.61	92.62	338.12	8.15	13.85	26.28	7.70	12.47	2.88
STDEV	2.89	3.32	11.58	.42	.64	.35	3.93	2.76	3.14
VALID	5	5	5	5	5	5	5	4	4
3									
MEAN	10.57	87.37	325.35	7.89	11.60	26.42	5.25	15.85	3.74
STDEV	1.85	1.97	6.54	.13	1.53	1.13	2.06	5.08	2.51
VALID	4	4	4	4	4	4	4	4	4
4									
MEAN	12.70	90.04	331.37	7.75	11.30	26.26	15.95	14.76	1.65
STDEV	1.98	5.53	6.28	.35	.82	1.64	11.50	6.52	2.15
VALID	11	11	11	11	11	10	11	9	9
5									
MEAN	5.30	95.13	334.48	7.72	12.45	26.61	102.00	25.50	.25
STDEV	.61	5.14	3.67	.21	.21	1.27	0	5.23	.05
VALID	4	4	4	2	4	4	4	2	2
SEASONALLY WEIGHTED MEAN	8.6	92.6	324.8	7.8	12.7	26.5	54.0	26.3	1.28

TABLE 3a: Physical variables. Concentrations within the five seasonal thermal periods. Station 41, 1982.

Seasonal Thermal Period		EBT °C	ALKA $G.M^{-3}$	COND UMHOS	pH	DISSO2 $G.M^{-3}$	CL $G.M^{-3}$	MIXED DEPTH M	EUPHOTIC DEPTH M	RATIO DZ/DM M
1										
	MEAN	2.11	94.41	320.86	7.82	13.86	26.65	126.00	35.00	.28
	STDEV	1.08	3.97	14.71	.44	.12	.21	0	6.42	.05
	VALION	14	14	14	12	14	13	14	9	9
2										
	MEAN	13.94	93.77	330.13	8.28	12.84	26.24	8.83	12.43	2.33
	STDEV	1.38	.34	5.42	.21	.38	.24	5.84	1.86	2.14
	VALION	3	3	3	3	3	3	3	3	3
3										
	MEAN	19.83	85.47	316.07	8.10	10.84	26.48	7.00	18.05	2.57
	STDEV	.84	3.47	12.41	.26	.83	.12	1.87	8.51	1.32
	VALION	4	4	4	4	4	4	5	4	4
4										
	MEAN	14.86	87.15	324.79	7.70	10.89	25.48	18.78	16.66	.97
	STDEV	2.56	6.49	6.77	.40	.91	.79	6.32	8.01	.45
	VALION	9	9	9	9	9	9	9	9	9
5										
	MEAN	6.95	95.14	331.24	7.77	12.03	26.12	126.00	23.30	.19
	STDEV	1.34	3.31	2.95	.12	.40	.37	0	13.79	.11
	VALION	5	5	5	3	5	5	5	4	4
SEASONALLY WEIGHTED MEAN		9.1	91.7	322.6	7.9	12.4	26.3	74.2	29.2	1.01

TABLE 3a: Physical variables. Concentrations within the five seasonal thermal periods. Station 81, 1982.

Seasonal Thermal Period	EBT °C	ALKA $G.M^{-3}$	COND UMHOS	pH	DISSO2 $G.M^{-3}$	CL $G.M^{-3}$	MIXED DEPTH M	EUPHOTIC DEPTH M	RATIO DZ/DM M
1									
MEAN	2.86	93.73	324.18	7.81	14.25	25.91	35.00	16.86	.54
STDEV	1.93	4.35	18.91	.40	.13	.66	0	1.37	.04
VALION	4	4	4	4	4	4	4	4	4
2									
MEAN	11.94	94.13	326.94	8.05	12.31	25.99	12.50	18.65	1.69
STDEV	2.72	3.12	12.35	.42	.90	.72	4.80	2.32	.66
VALION	9	9	9	8	9	9	9	9	9
3									
MEAN	19.06	87.35	322.41	7.82	9.64	25.63	17.75	14.38	1.03
STDEV	1.58	4.28	8.34	.37	.56	.61	7.02	5.21	.77
VALION	10	10	10	10	10	10	10	9	9
4									
MEAN	11.60	89.89	326.08	7.71	10.65	25.87	29.94	17.16	.60
STDEV	2.45	5.91	7.82	.35	.61	.30	6.48	4.30	.22
VALION	9	9	9	7	9	9	9	9	9
SEASONALLY WEIGHTED MEAN	12.2	91.5	326.6	7.9	11.5	25.8	22.9	17.4	1.00

TABLE 3a: Physical variables. Concentrations within the five seasonal thermal periods. Station 93, 1982.

Seasonal Thermal Period	EBT °C	ALKA $G.M^{-3}$	COND UMHOS	pH	DISSO2 $G.M^{-3}$	CL $G.M^{-3}$	MIXED DEPTH M	EUPHOTIC DEPTH M	RATIO DZ/DM M
1									
MEAN	1.22	88.74	278.36	7.90	14.58	21.66	18.40	10.97	.56
STDEV	.60	10.23	22.37	.45	.46	3.58	3.23	5.99	.27
VALION	10	9	10	9	10	10	10	9	9
2									
MEAN	9.70	91.21	308.46	7.89	12.68	21.20	18.70	11.88	.62
STDEV	2.61	3.74	15.93	.47	.98	1.71	1.79	3.37	.11
VALION	5	5	5	4	5	5	5	5	5
3									
MEAN	19.83	89.85	304.77	7.92	10.32	22.06	12.45	12.30	1.25
STDEV	1.78	3.19	22.33	.34	1.00	1.64	6.17	3.07	.70
VALION	10	10	10	10	10	10	10	10	10
4									
MEAN	12.76	93.46	318.77	7.74	11.01	22.04	13.45	12.73	1.54
STDEV	2.49	4.69	14.47	.37	.54	2.44	6.78	7.24	1.84
VALION	11	11	11	10	11	11	11	11	11
5									
MEAN	5.06	92.02	328.50	M	12.06	25.66	16.00	16.20	1.01
STDEV	M	M	M	M	M	M	M	M	M
VALION	1	1	1	0	1	1	1	1	1
SEASONALLY WEIGHTED MEAN	10.9	90.7	300.0	7.9	12.1	21.7	25.7	17.3	0.85

TABLE 3b: **Chemical variables. Concentrations within the five seasonal thermal periods. Station 12, 1981.**

Seasonal Thermal Period		TP G.M^{-3}	TFP G.M^{-3}	TKJN G.M^{-3}	NH3 G.M^{-3}	NO3NO2 G.M^{-3}	SRS G.M^{-3}
1							
	MEAN	.014	.009	.174	.007	.350	.410
	STDEV	.011	.001	.019	.007	.012	.178
	VALION	9	9	9	9	9	9
2							
	MEAN	.019	.009	.213	.016	.194	.202
	STDEV	.003	.001	.040	.009	.106	.087
	VALION	7	7	7	7	7	7
3							
	MEAN	.018	.008	.254	.017	.077	.127
	STDEV	.005	.001	.036	.010	.047	.048
	VALION	11	11	11	11	11	11
4							
	MEAN	.012	.006	.214	.005	.250	.347
	STDEV	.002	.001	.039	.003	.079	.122
	VALION	6	6	6	6	6	6
5							
	MEAN	.011	.007	.188	.009	.315	.372
	STDEV	.001	.001	.017	.004	.027	.093
	VALION	5	5	5	5	5	5
SEASONALLY WEIGHTED MEAN		0.015	0.008	0.214	0.011	0.219	0.272

TABLE 3b: **Chemical variables. Concentrations within the five seasonal thermal periods. Station 41, 1981.**

Seasonal Thermal Period		TP $G.M^{-3}$	TFP $G.M^{-3}$	TKJN $G.M^{-3}$	NH3 $G.M^{-3}$	NO3NO2 $G.M^{-3}$	SRS $G.M^{-3}$
1							
	MEAN	.013	.008	.173	.006	.337	.258
	STDEV	.003	.001	.012	.003	.013	.081
	VALION	12	12	12	10	12	11
2							
	MEAN	.016	.007	.210	.009	.175	.358
	STDEV	.001	.001	.015	.003	.046	.014
	VALION	4	4	4	4	4	4
3							
	MEAN	.016	.007	.221	.006	.060	.095
	STDEV	.002	.001	.020	.003	.032	.047
	VALION	10	10	10	10	10	10
4							
	MEAN	.011	.006	.208	.004	.227	.237
	STDEV	.001	.001	.020	.002	.034	.053
	VALION	9	9	9	9	9	9
5							
	MEAN	.011	.007	.185	.004	.284	.316
	STDEV	.001	.001	.011	.002	.023	.079
	VALION	3	3	3	3	3	3
SEASONALLY WEIGHTED MEAN		0.014	0.007	0.200	0.006	0.211	0.190

TABLE 3b: **Chemical variables. Concentrations within the five seasonal thermal periods. Station 81, 1981.**

Seasonal Thermal Period		TP $G.M^{-3}$	TFP $G.M^{-3}$	TKJN $G.M^{-3}$	NH3 $G.M^{-3}$	NO3NO2 $G.M^{-3}$	SRS $G.M^{-3}$
1							
	MEAN	.013	3.70E-.005	.190	.006	.267	.111
	STDEV	.001	.004	.023	.002	.016	.126
	VALION	8	8	8	7	8	8
2							
	MEAN	.012	.006	.211	.012	.227	.056
	STDEV	.002	.001	.025	.005	.043	.032
	VALION	8	8	8	8	8	7
3							
	MEAN	.016	.008	.249	.013	.059	.148
	STDEV	.002	.001	.020	.009	.022	.043
	VALION	11	11	11	11	11	11
4							
	MEAN	.015	.008	.221	.007	.178	.340
	STDEV	.002	.001	.023	.003	.025	.042
	VALION	9	9	9	9	9	9
5							
	MEAN	.014	.008	.204	.009	.231	.321
	STDEV	5.77E-.005	2.52E-.004	.027	.006	.025	.011
	VALION	3	3	3	3	3	3
SEASONALLY WEIGHTED MEAN		0.014	0.007	0.220	0.010	0.169	0.171

TABLE 3b: **Chemical variables. Concentrations within the five seasonal thermal periods. Station 93, 1981.**

Seasonal Thermal Period	TP G.M^{-3}	TFP G.M^{-3}	TKJN G.M^{-3}	NH3 G.M^{-3}	NO3NO2 G.M^{-3}	SRS G.M^{-3}
1						
MEAN	.017	.006	.202	.016	.305	.194
STDEV	.004	.001	.029	.011	.030	.065
VALION	7	7	7	7	7	7
2						
MEAN	.017	.007	.218	.022	.292	.180
STDEV	.003	.002	.018	.009	.082	.034
VALION	7	7	7	7	7	7
3						
MEAN	.016	.007	.241	.022	.138	.190
STDEV	.003	.001	.026	.012	.058	.060
VALION	13	13	13	12	13	13
4						
MEAN	.016	.007	.235	.018	.150	.200
STDEV	.005	.002	.028	.011	.039	.064
VALION	8	8	8	8	8	8
5						
MEAN	.017	.006	.218	.017	.251	.237
STDEV	.002	4.73E-004	.028	.012	.056	.043
VALION	3	3	3	3	3	3
SEASONALLY WEIGHTED MEAN	0.016	0.007	0.227	0.020	0.205	0.178

TABLE 3b: **Chemical variables. Concentrations within the five seasonal thermal periods. Station 12, 1982.**

Seasonal Thermal Period	TP $G.M^{-3}$	TFP $G.M^{-3}$	SRP $G.M^{-3}$	TKJN $G.M^{-3}$	NH3 $G.M^{-3}$	NO3NO2 $G.M^{-3}$	SRS $G.M^{-3}$
1							
MEAN	.013	.010	.003	.221	.011	.342	.485
STDEV	.001	.001	.002	.037	.013	.021	.063
VALID	9	9	12	11	13	13	13
2							
MEAN	.016	.007	.001	.268	.012	.191	.144
STDEV	.003	.001	2.07E-004	.050	.006	.079	.062
VALID	5	5	5	5	5	5	5
3							
MEAN	.011	.007	.002	.324	.030	.162	.163
STDEV	.001	.001	.001	.035	.011	.040	.097
VALID	4	4	4	4	4	4	4
4							
MEAN	.015	.007	.001	.341	.042	.211	.212
STDEV	.002	.001	.001	.068	.025	.046	.070
VALID	11	11	11	11	11	11	11
5							
MEAN	.013	.007	.002	.341	.027	.351	.514
STDEV	.004	.002	.002	.085	.010	.024	.121
VALID	4	4	4	4	4	4	4
SEASONALLY WEIGHTED MEAN	0.014	0.008	0.002	0.286	0.024	0.265	0.325

TABLE 3b: **Chemical variables. Concentrations within the five seasonal thermal periods. Station 41, 1982.**

Seasonal Thermal Period	TP $G.M^{-3}$	TFP $G.M^{-3}$	SRP $G.M^{-3}$	TKJN $G.M^{-3}$	NH3 $G.M^{-3}$	NO3NO2 $G.M^{-3}$	SRS $G.M^{-3}$
1							
MEAN	.013	.009	.003	.217	.009	.334	.414
STDEV	4.00E-004	.001	.002	.048	.007	.024	.052
VALION	10	10	14	13	14	14	14
2							
MEAN	.017	.007	.002	.251	.004	.194	.130
STDEV	.006	.002	.001	.063	.003	.130	.062
VALION	3	3	3	3	3	3	3
3							
MEAN	.012	.008	.001	.296	.035	.110	.085
STDEV	.003	.003	.001	.034	.017	.012	.007
VALION	4	4	4	4	4	4	4
4							
MEAN	.015	.008	.001	.364	.042	.173	.169
STDEV	.003	.002	4.29E-004	.092	.025	.038	.133
VALION	9	9	9	9	9	9	9
5							
MEAN	.011	.007	.001	.301	.021	.308	.400
STDEV	.001	.002	.001	.037	.014	.033	.143
VALION	5	5	5	5	5	5	5
SEASONALLY WEIGHTED MEAN	0.013	0.008	0.002	0.273	0.021	0.251	0.290

TABLE 3b: **Chemical variables. Concentrations within the five seasonal therma' periods. Station 81, 1982.**

Seasonal Thermal Period	TP $G.M^{-3}$	TFP $G.M^{-3}$	SRP $G.M^{-3}$	TKJN $G.M^{-3}$	NH3 $G.M^{-3}$	NO3NO2 $G.M^{-3}$	SRS $G.M^{-3}$
1							
MEAN	.013	.005	.001	.215	.007	.287	.174
STDEV	0	.001	2.94E-004	.014	.004	.029	.048
VALIDN	2	2	4	2	4	4	4
2							
MEAN	.013	.006	.001	.277	.013	.213	.101
STDEV	.002	.001	3.57E-004	.044	.010	.043	.076
VALIDN	7	7	9	9	9	9	9
3							
MEAN	.017	.009	.001	.332	.051	.102	.214
STDEV	.003	.003	.001	.056	.032	.036	.098
VALIDN	10	10	10	10	10	10	10
4							
MEAN	.017	.008	.001	.344	.037	.178	.457
STDEV	.002	.002	.001	.084	.018	.044	.134
VALIDN	9	9	8	9	9	9	9
SEASONALLY WEIGHTED MEAN	0.015	0.007	0.001	0.309	0.028	0.186	0.235

TABLE 3b: **Chemical variables. Concentrations within the five seasonal thermal periods. Station 93, 1982.**

Seasonal Thermal Period	TP $G.M^{-3}$	TFP $G.M^{-3}$	SRP $G.M^{-3}$	TKJN $G.M^{-3}$	NH3 $G.M^{-3}$	NO3NO2 $G.M^{-3}$	SRS $G.M^{-3}$
1							
MEAN	.019	.008	.002	.226	.029	.327	.321
STDEV	.003	.001	.002	.025	.021	.024	.102
VALION	11	10	11	10	11	10	11
2							
MEAN	.016	.007	.001	.122	.036	.285	.142
STDEV	4.00E-004	.002	3.36E-004	.051	.018	.035	.057
VALION	3	3	5	5	5	5	5
3							
MEAN	.015	.008	.001	.320	.046	.170	.172
STDEV	.002	.002	.001	.065	.036	.032	.053
VALION	10	10	10	10	10	10	9
4							
MEAN	.018	.009	.001	.168	.043	.223	.335
STDEV	.006	.003	.001	.075	.017	.057	.154
VALION	12	12	12	12	12	12	12
SEASONALLY WEIGHTED MEAN	0.017	0.008	0.001	0.308	0.039	0.245	0.252

TABLE 3c: **Biological variables. Concentrations within the five seasonal thermal periods. Station 12, 1981.**

Seasonal Thermal Period	IPON G.M^{-3}	IPOC G.M^{-3}	ICHLAU G.M^{-3}	ICHLAC G.M^{-3}	DOC G.M^{-3}	DRY WEIGHT G.M^{-3}	LOI G.M^{-3}
1							
MEAN	.03389	.21389	2.725	2.488	2.13042	.36667	.54000
STDEV	.01173	.05419	1.537	1.303	.26457	.65625	.39115
VALION	9	9	8	8	9	6	5
2							
MEAN	.12214	.73100	5.729	5.471	2.20434	2.06000	1.72500
STDEV	.05041	.30488	3.196	3.073	.07508	1.24218	1.40801
VALION	7	7	7	7	7	5	4
3							
MEAN	.12689	.67480	5.170	4.400	2.59022	2.45000	2.20000
STDEV	.04277	.21817	3.071	2.925	.36093	1.29979	.78558
VALION	9	10	10	10	11	10	8
4							
MEAN	.06450	.42533	4.517	3.917	2.05628	1.36667	.45000
STDEV	.01875	.11574	1.189	1.005	.10913	.26563	.12910
VALION	6	6	6	6	6	6	4
5							
MEAN	.04300	.25067	3.225	2.450	1.99176	1.00000	.66667
STDEV	.00721	.02574	1.242	1.133	.04062	.14142	.11547
VALION	3	3	4	4	5	4	3
Seasonally Weighted Mean	.083	.485	4.5	4.0	2.3	1.842	1.343

TABLE 3c: **Biological variables. Concentrations within the five seasonal thermal periods. Station 41, 1981.**

Seasonal Thermal Period		IPON G.M^{-3}	IPOC G.M^{-3}	ICHLAU G.M^{-3}	ICHLAC G.M^{-3}	DOC G.M^{-3}	DRY WEIGHT G.M^{-3}	LOI G.M^{-3}
1								
	MEAN	.03420	.21310	3.040	2.770	2.18456	.6000	.25000
	STDEV	.00612	.02864	1.451	1.372	.12555	.49800	.28868
	VALION	10	10	10	10	12	5	4
2								
	MEAN	.10833	.68667	4.425	4.350	2.09540	1.37500	M
	STDEV	.01234	.06123	.737	.806	.06687	.34034	M
	VALION	3	3	4	4	4	4	0
3								
	MEAN	.10300	.63390	3.880	3.590	2.49623	2.93000	2.07500
	STDEV	.01780	.09585	1.482	1.479	.32957	1.18514	.31053
	VALION	10	10	10	10	10	10	8
4								
	MEAN	.06200	.38656	4.778	4.211	2.05780	1.14444	.90000
	STDEV	.00809	.05737	1.392	1.344	.10030	.32059	.06165
	VALION	9	9	9	9	9	9	4
5								
	MEAN	.04000	.23700	3.700	3.100	2.02877	.70000	M
	STDEV	M	M	M	M	.02584	M	M
	VALION	1	1	1	1	3	1	0
Seasonally Weighted Mean		.073	.444	3.9	3.6	2.2	1.462	-

TABLE 3c: **Biological variables. Concentrations within the five seasonal thermal periods. Station 81, 1981.**

Seasonal Thermal Period	IPON G.M^{-3}	IPOC G.M^{-3}	ICHLAU G.M^{-3}	ICHLAC G.M^{-3}	DOC G.M^{-3}	DRY WEIGHT G.M^{-3}	LOI G.M^{-3}
1							
MEAN	.07988	.50038	6.914	6.614	2.34406	1.88000	1.48000
STDEV	.00594	.05380	2.075	2.218	.29770	.31145	.34928
VALIDN	8	8	7	7	8	5	5
2							
MEAN	.05781	.56138	4.738	4.581	2.30425	1.48333	1.27500
STDEV	.01952	.07700	2.499	2.419	.09540	.22286	.25000
VALIDN	8	8	8	8	8	6	4
3							
MEAN	.10365	.54336	6.155	5.609	2.63886	2.54545	2.00000
STDEV	.02138	.09225	1.786	1.546	.26679	1.24126	.40708
VALIDN	11	11	11	11	11	11	8
4							
MEAN	.06256	.35867	5.344	4.511	2.10877	1.65000	1.12857
STDEV	.01647	.08367	1.271	1.456	.12545	.31807	.31472
VALIDN	9	9	9	9	9	8	7
5							
MEAN	.05000	.23967	5.667	5.000	1.99543	2.00000	.93333
STDEV	.00436	.02511	1.504	1.697	.03706	.26458	.05774
VALIDN	3	3	3	3	3	3	3
Seasonally Weighted Mean	.084	.479	5.7	5.2	2.4	1.995	1.482

TABLE 3c: **Biological variables. Concentrations within the five seasonal thermal periods. Station 93, 1981.**

Seasonal Thermal Period	IPON G.M^{-3}	IPOC G.M^{-3}	ICHLAU G.M^{-3}	ICHLAC G.M^{-3}	DOC G.M^{-3}	DRY WEIGHT G.M^{-3}	LOI G.M^{-3}
1							
MEAN	.06817	.48950	4.243	3.643	2.24464	3.50000	1.40000
STDEV	.01462	.07893	1.393	1.365	.35388	.78316	.37417
VALION	6	6	7	7	7	4	4
2							
MEAN	.11314	.60557	5.214	4.614	2.28964	3.30000	1.62500
STDEV	.03752	.14900	2.186	2.041	.11746	1.74547	.51235
VALION	7	7	7	7	7	4	4
3							
MEAN	.09029	.48071	4.214	3.643	2.42142	2.55714	1.40000
STDEV	.03412	.08681	1.096	.980	.26089	.84431	.23094
VALION	7	7	7	7	13	7	7
4							
MEAN	.07300	.47450	5.250	4.125	2.18071	6.05000	1.52500
STDEV	.01347	.09326	.311	.435	.16841	3.59398	.35000
VALION	4	4	4	4	8	4	4
5							
MEAN	M	M	M	M	2.06720	M	M
STDEV	M	M	M	M	.10409	M	M
VALION	0	0	0	0	3	0	0
Seasonally Weighted Mean	.082	.476	4.6	3.9	2.3	3.661	1.520

TABLE 3c: **Biological variables. Concentrations within the five seasonal thermal periods. Station 12, 1982.**

Seasonal Thermal Period		IPON $G.M^{-3}$	IPOC $G.M^{-3}$	DOC $G.M^{-3}$	DRY WEIGHT $G.M^{-3}$	LOI $G.M^{-3}$
1						
	MEAN	.021	.149	1.998	1.644	.625
	STDEV	.004	.022	.096	2.353	.096
	VALION	10	10	13	9	4
2						
	MEAN	.118	.741	2.177	2.100	1.967
	STDEV	.038	.144	.223	.816	.586
	VALION	4	4	5	4	3
3						
	MEAN	.065	.382	2.427	2.600	1.650
	STDEV	.006	.040	.355	.566	.212
	VALION	2	2	4	2	2
4						
	MEAN	.072	.415	2.157	1.900	1.390
	STDEV	.025	.112	.146	.464	.354
	VALION	10	10	11	10	10
5						
	MEAN	.029	.245	2.093	.850	.725
	STDEV	.009	.122	.114	.208	.206
	VALION	4	4	4	4	4
SEASONALLY WEIGHTED MEAN		0.056	0.343	2.1	1.818	1.144

TABLE 3c: **Biological variables. Concentrations within the five seasonal thermal periods. Station 41, 1982.**

Seasonal Thermal Period	IPON G.M^{-3}	IPOC G.M^{-3}	DOC G.M^{-3}	DRY WEIGHT G.M^{-3}	LOI G.M^{-3}
1					
MEAN	.022	.141	2.001	.742	.533
STDEV	.006	.036	.088	.429	.437
VALID	13	13	14	12	6
2					
MEAN	.098	.568	2.208	1.800	1.400
STDEV	.011	.025	.051	.173	.566
VALID	3	3	3	3	2
3					
MEAN	.078	.366	2.191	1.500	1.133
STDEV	.009	.085	.179	.100	.153
VALID	3	3	4	3	3
4					
MEAN	.062	.397	2.311	1.725	1.450
STDEV	.020	.105	.351	.748	.571
VALID	8	8	9	8	8
5					
MEAN	.031	.201	2.320	.720	.600
STDEV	.006	.038	.152	.164	.187
VALID	5	5	5	5	5
SEASONALLY WEIGHTED MEAN	0.048	0.282	2.2	1.168	0.920

TABLE 3c: **Biological variables. Concentrations within the five seasonal thermal periods. Station 81, 1982.**

Seasonal Thermal Period	IPON $G.M^{-3}$	IPOC $G.M^{-3}$	DOC $G.M^{-3}$	DRY WEIGHT $G.M^{-3}$	LOI $G.M^{-3}$
1					
MEAN	.061	.366	2.285	1.500	1.100
STDEV	.013	.104	.179	.265	.100
VALIDN	4	4	4	3	3
2					
MEAN	.082	.465	2.367	1.571	1.550
STDEV	.023	.146	.265	.655	.636
VALIDN	7	7	9	7	2
3					
MEAN	.077	.420	2.297	2.070	1.600
STDEV	.028	.125	.163	.702	.435
VALIDN	10	10	10	10	10
4					
MEAN	.060	.347	2.360	1.588	1.038
STDEV	.022	.092	.234	.726	.262
VALIDN	8	8	9	8	8
SEASONALLY WEIGHTED MEAN	0.071	0.400	2.3	1.707	1.350

TABLE 3c: **Biological variables. Concentrations within the five seasonal thermal periods. Station 93, 1982.**

Seasonal Thermal Period		IPON G.M^{-3}	IPOC G.M^{-3}	DOC G.M^{-3}	DRY WEIGHT G.M^{-3}	LOI G.M^{-3}
1						
	MEAN	.044	.274	2.167	5.022	1.367
	STDEV	.012	.064	.212	4.668	.592
	VALIDN	11	11	11	9	9
2						
	MEAN	.084	.479	2.275	2.400	1.340
	STDEV	.008	.057	.135	.667	.297
	VALIDN	5	5	5	5	5
3						
	MEAN	.092	.487	2.349	2.700	1.722
	STDEV	.027	.139	.192	.687	.373
	VALIDN	9	9	10	9	9
4						
	MEAN	.055	.365	2.336	5.033	1.742
	STDEV	.025	.174	.377	6.445	1.087
	VALIDN	12	12	12	12	12
SEASONALLY WEIGHTED MEAN		0.065	0.380	2.3	4.028	1.569

For the majority of the year the pH of Lake Ontario ranged from 7.7 to 7.8, but during periods two and three it increased by 0.2 to 0.5 pH units. Alkalinity, on the other hand, fell from 95 $gCaCO_3.m^{-3}$ in the spring, to approximately 85 $gCaCO_3.m^{-3}$ in period three, and rose again in the following two periods. Conductivity was steady throughout the year at station 41 with a seasonally weighted mean of 323 µmhos. At station 12 conductivity was lower in period one than during the rest of the year; 313 µmhos as compared with 325 to 338 µmhos. Chloride was constant at 26 $g.m^{-3}$ at all times.

The shallowness of the nearshore stations, 81 and 93, greatly affects the development of their thermal structure. The thermocline develops at station 81 in early to mid-May. Water temperature rises rapidly in the spring reaching 8° to 12°C at stratification, and peaks in late July to early August at just above 20°C. The depth of the mixed layer varies erratically over the summer, eroding dramatically from mid-August until turnover in October. A stable thermocline does not exist at station 93, which is not only the shallowest station, but also situated two to three km off shore. Distinct thermal stratification occurs erratically from June until November. Thus the temperature regime and stratification are uncoupled. Water temperatures rise steeply in May and June reaching maximal levels near 22°C in July and August.

Oxygen concentrations also fell at these nearshore stations as water temperatures increased. Minimal levels of 9.1 to 10.1 $g.m^{-3}$ were observed during August. Percent saturation increased in periods two and three but not by as much as at the mid-lake stations. It ranged from 108 to 117 percent as compared with the 122 to 132 percent observed offshore.

The seasonal behaviour of the euphotic depth differed considerably between the nearshore and offshore stations. The euphotic depth varied only slightly through the year ranging from 10 to 19 m (Table 3a). The shallowest values at station 81 were again observed in period three. The ratio of DZ/DM was periodically greater than one during periods two to four, but otherwise averaged around 0.7. There was no distinct minimal period at station 93.

The seasonal patterns and concentrations of pH, alkalinity and conductivity at station 81 were similar to those of the mid-lake stations (Table 3a). Although alkalinity also followed mid-lake patterns at station 93, the other parameters did not. Conductivity increased steadily through the year from 276 µmhos in the spring to 328 µmhos in late autumn (period five). pH increased only by 0.1 pH unit during periods one to three. The chloride concentration was lowered by the plume of the Niagara River from 26 $g.m^{-3}$ to 22 $g.m^{-3}$ (Table 3a).

The parameters were grouped into seasonal thermal periods, and the effects of station location, season and year were examined using a three- or two-way analysis of variance. As expected, all variables changed significantly throughout the year with the exceptions of CL and COND (stations 41 and 81, only) (Table 4). The only physical variable to differ significantly between years was temperature. The seasonally weighted mean was 1.5° to 2.1°C higher in 1981 than in 1982 at stations 12, 41 and 93 (Table 3a). There was no difference at station 81. Dissolved oxygen, CL and COND were significantly different amongst stations. Oxygen concentrations were lower in thermal period three at the nearshore stations than at the mid-lake stations (Table 3a) while chloride and conductivity were 15 and 8 percent lower, respectively, at station 93 than at the other stations.

TABLE 4: Influence of station location (St.), season (Se.), and year (Yr.) on the variability of physical, nutrient, and biological parameters. The results of the three- or two- (pH, SRP, CHLA-U, CHLA-C, COND) way analysis of variance are indicated as follows: $p > 0.05$ n.s., $0.05 > p < 0.01$ *, $0.01 > p < 0.001$ ** and $p < 0.001$ ***. A dash indicates no comparison.

	Probability of No Effect						
Parameter	Station	Season	Year	Interaction St.-Se.	Interaction St.-Yr.	Interaction Se.-Yr.	No. of Cases
Physical							
EBT	n.s.	***	*	n.s.	n.s.	***	263
ALKA	n.s.	***	n.s.	***	n.s.	***	263
$DISSO_2$	***	***	n.s.	***	n.s.	n.s.	263
CL	***	n.s.	n.s.	n.s.	n.s.	n.s.	256
pH	n.s.	*	–	***	–	–	143
COND	***	***	–	***	–	–	143
DM	***	***	n.s.	***	n.s.	n.s.	302
DZ	n.s.	***	n.s.	n.s.	n.s.	n.s.	302
DZ/DM	n.s.	***	n.s.	n.s.	n.s.	n.s.	302
ELR	*	***	*	n.s.	n.s.	**	302
Nutrient							
TP	***	**	n.s.	***	n.s.	***	242
SRP	n.s.	***	–	n.s.	–	–	125
TFP	n.s.	***	***	***	*	n.s.	242
TKJN	n.s.	***	***	n.s.	n.s.	***	242
NO2NO3	***	***	***	***	n.s.	*	242
NH_3	***	***	***	n.s.	n.s.	***	242
SRS	***	***	***	***	**	**	242
Biological							
DOC	n.s.	***	n.s.	n.s.	n.s.	***	253
IPOC	n.s.	***	***	n.s.	n.s.	n.s.	223
IPON	n.s.	***	***	n.s.	n.s.	n.s.	223
ICHLAU	***	n.s.	–	n.s.	–	–	132
ICHLAC	***	n.s.	–	n.s.	–	–	132
SWD (all stations)	***	n.s.	n.s.	n.s.	n.s.	n.s.	191
(Stations 12,41,81)	n.s.	***	*	n.s.	n.s.	**	137
LOI (all stations)	*	***	n.s.	***	n.s.	n.s.	191
(Stations 12,41,81)	n.s.	***	n.s.	**	n.s.	**	137

Nutrient Regime

The nutrients can be divided into three groups based on their seasonal patterns: 1) those that decrease in the summer; 2) those that increase, reaching maxima in the summer; and 3) those with no distinct seasonal pattern.

The first group consists of SRS, SRP, and NO3NO2. The concentration of SRS was high in late autumn and spring, with values ranging from 0.237 to 0.514 $gSiO_2.m^{-3}$. At the nearshore stations minimum levels could occur early in the spring, but did not persist as long as those at the mid-lake stations (Table 3b) (Figs. 3a, 3b). Minimum silica concentrations were always observed in period two, and ranged from 0.050 to 0.144 $gSiO_2.m^{-3}$ in 1982 and from 0.056 to 0.127 $gSiO_2.m^{-3}$ in 1981. These low levels extended into period three and sometimes period four at the mid-lake stations (Table 3b). The analysis of variance results indicated that the levels of silica differed significantly amongst stations. It is not clear whether this resulted from differences in the timing of seasonal events relative to the thermal periods and/or from the lower winter levels at station 93 (cf. Fig. 3b). Levels at station 93 ranged from 0.237 to 0.314 $gSiO_2.m^{-3}$ as compared with 0.400 to 0.514 $gSiO_2.m^{-3}$ at the other stations. Silica levels also differed significantly between years. The seasonally weighted mean (SWM) values in 1981 were 20 to 34 percent lower than those in 1982. In 1982 the seasonally weighted mean values for stations 12, 41, 81 and 93, were respectively, 0.328, 0.290, 0.235, and 0.256 $gSiO_2.m^{-3}$, while in 1981 they were 0.262, 0.190, 0.171 and 0.178 $gSiO_2.m^{-3}$. This difference is undoubtedly associated with the larger standing crop of diatoms produced in 1981.

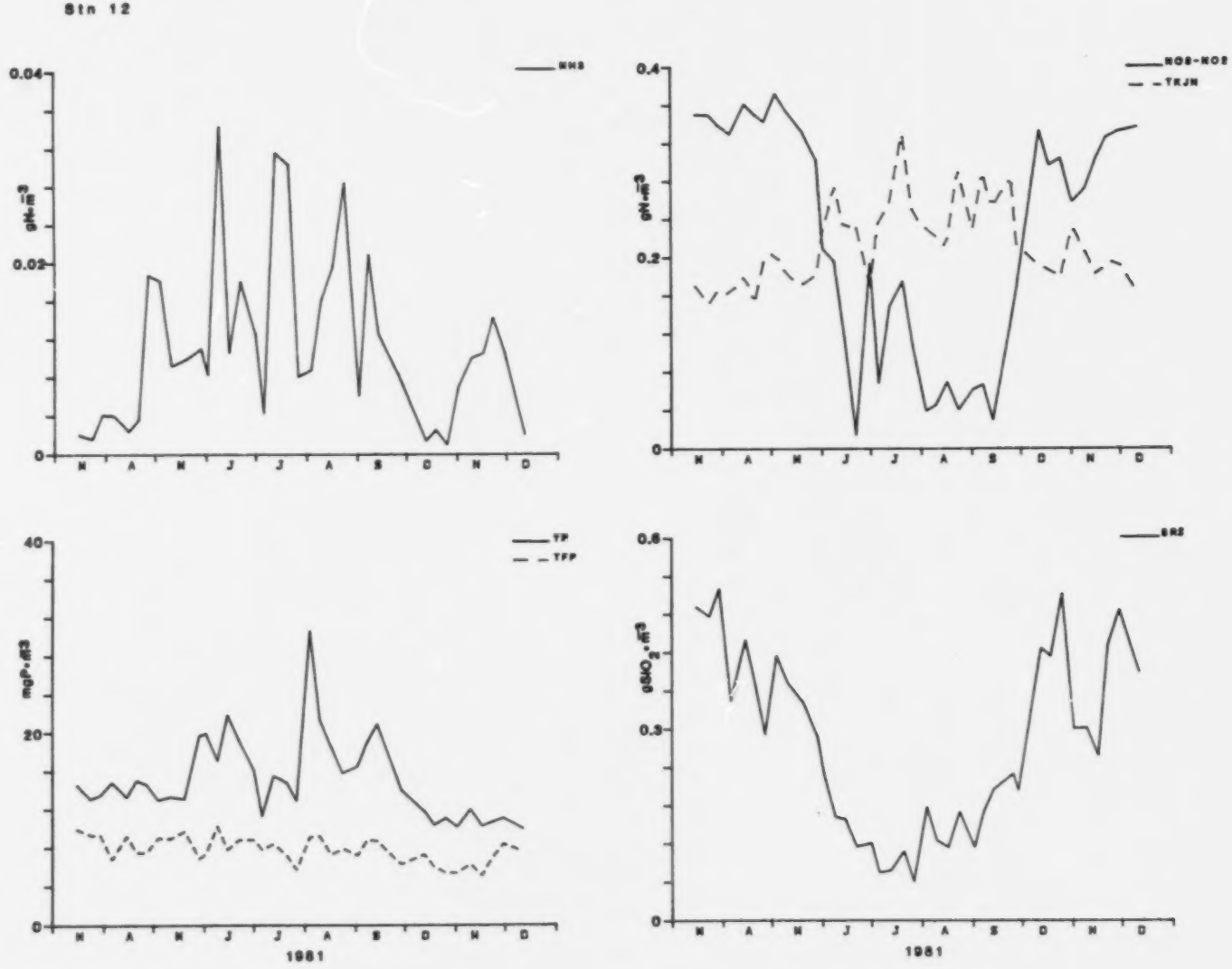


Figure 3a. Seasonal trends in NH3, TKJN, NO3NO2, SRS, SRP, TP, TFP, POC, PON, CHLAU and CHLAC at the four BioIndex stations in 1981.

Stn 41

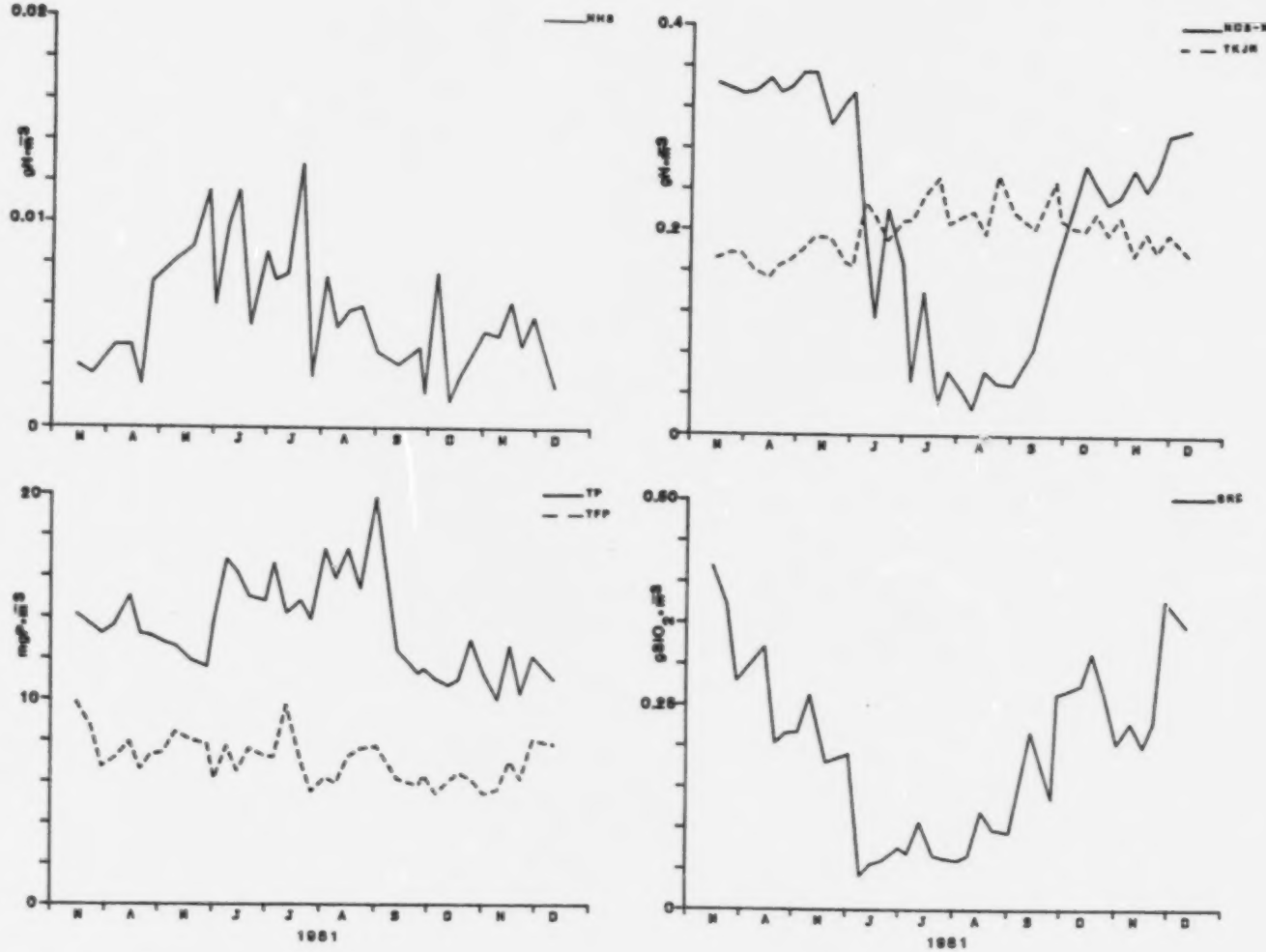


Figure 3a. (cont.)

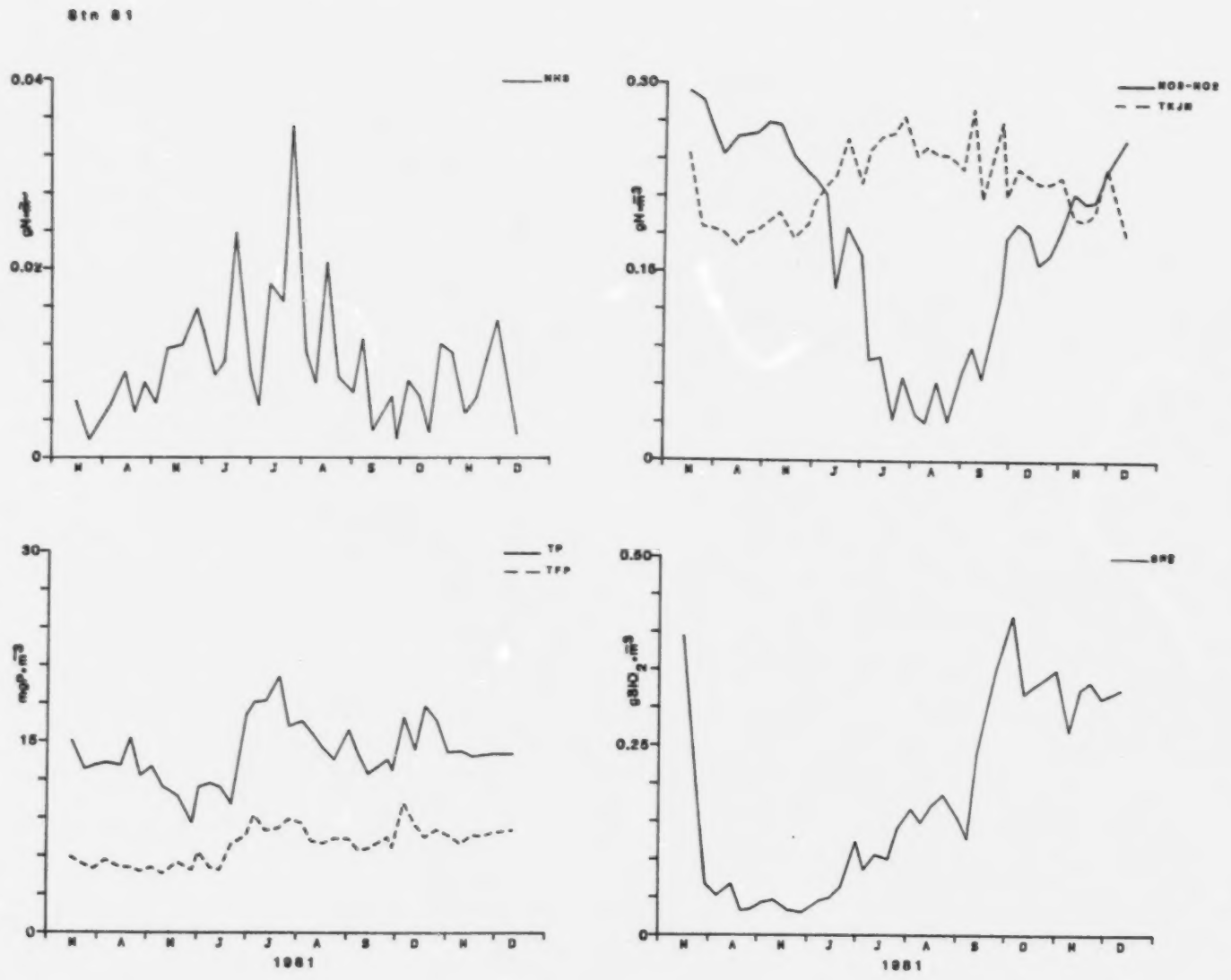


Figure 3a. (cont.)

Stn 93

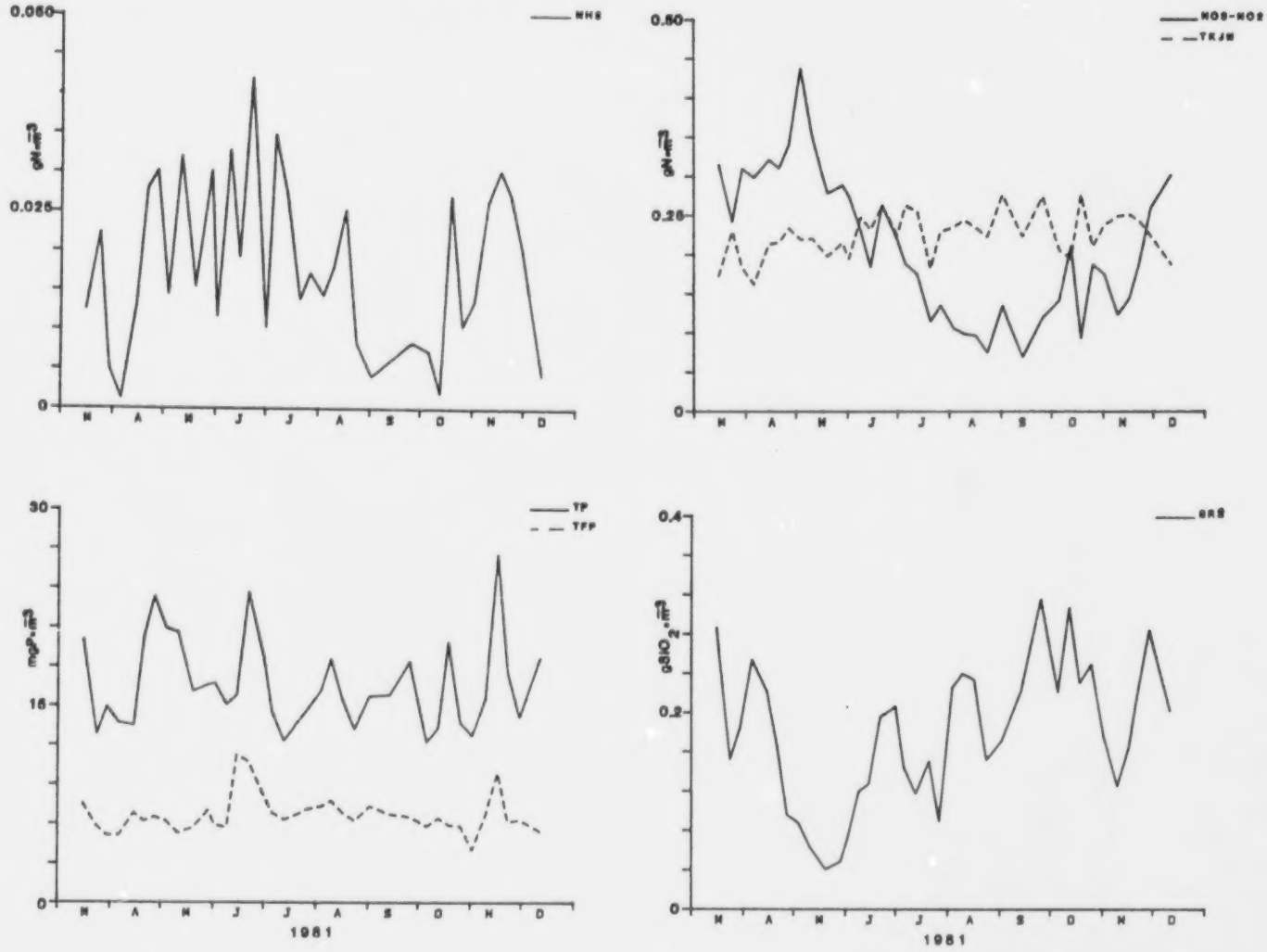


Figure 3a. (cont.)

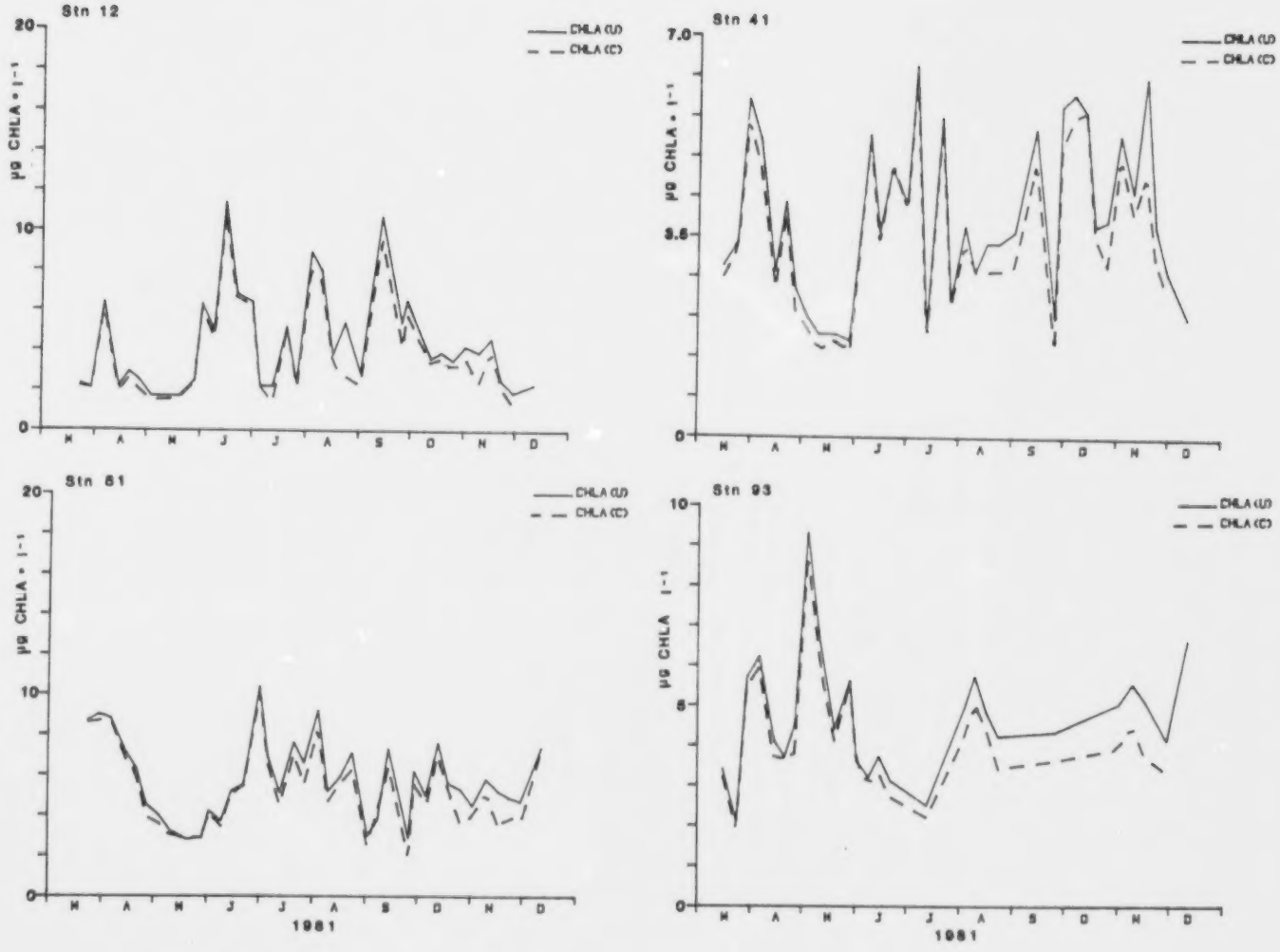


Figure 3a. (cont.)

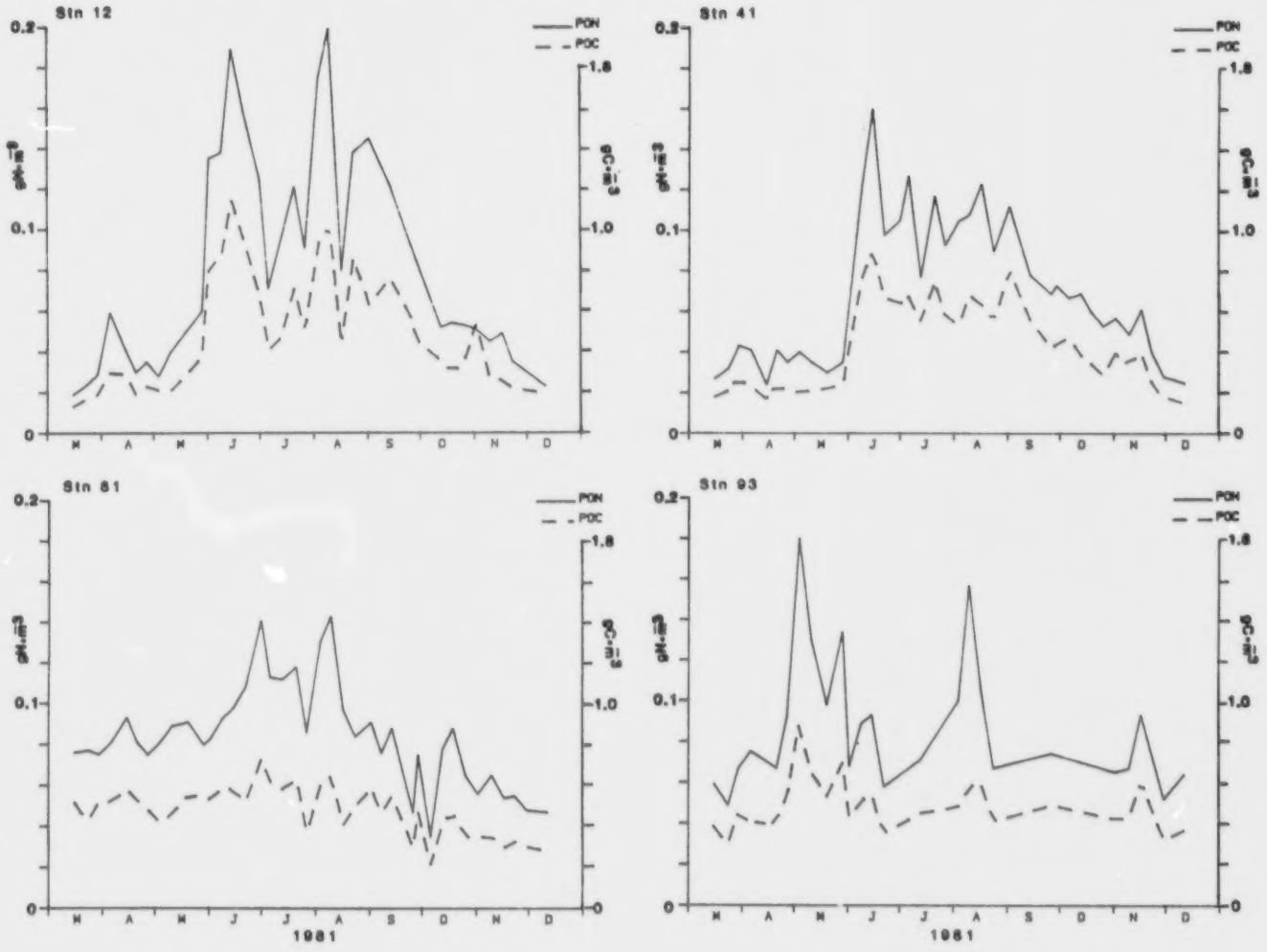


Figure 3a. (cont.)

Stn 12

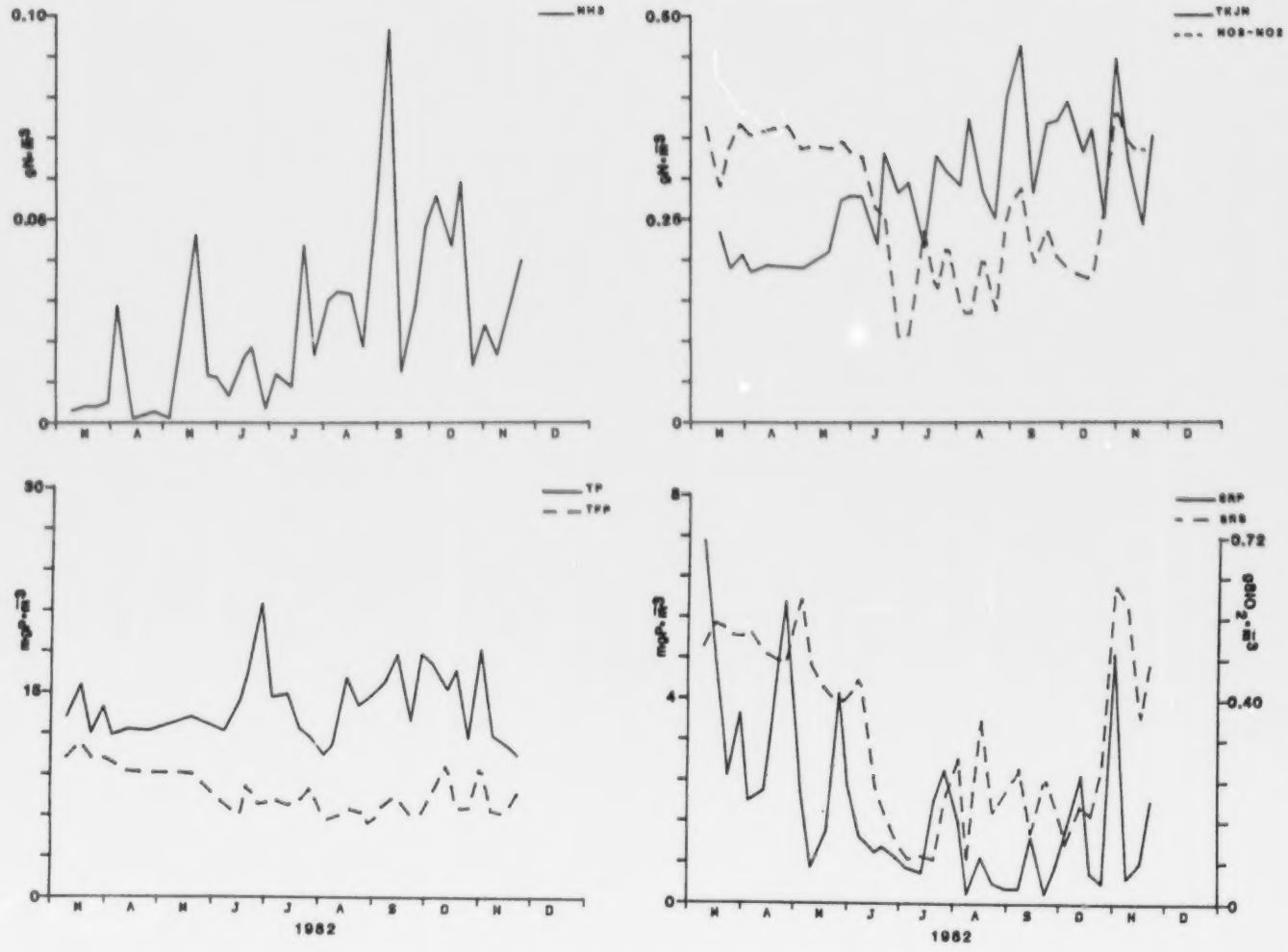


Figure 3b. Seasonal trends in NH3, TKJN, NO3NO2, SRS, SRP, TP, TFP, POC and PON at the four BioIndex stations in 1982.

Stn 41

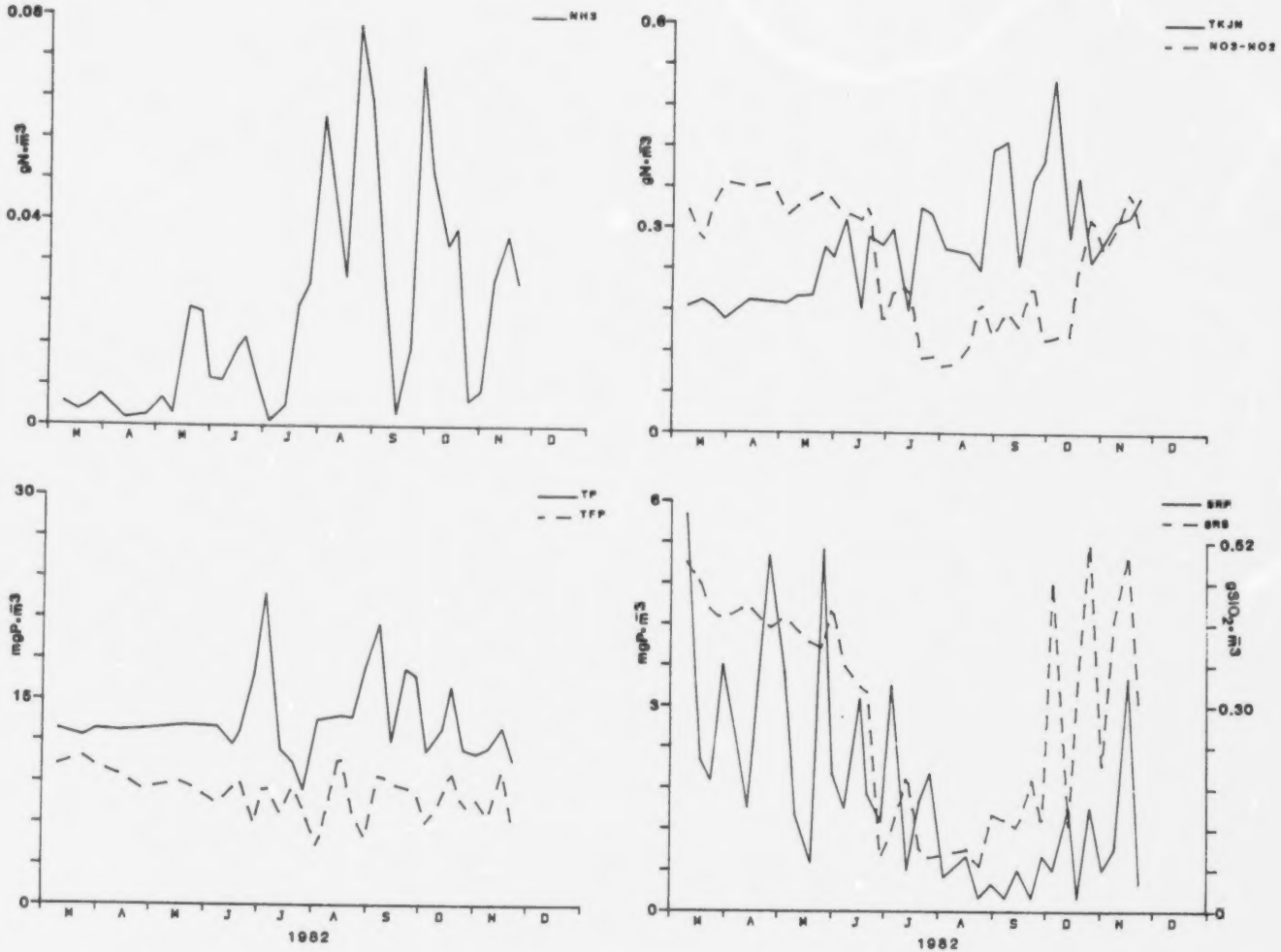


Figure 3b. (cont.)

Stn 81

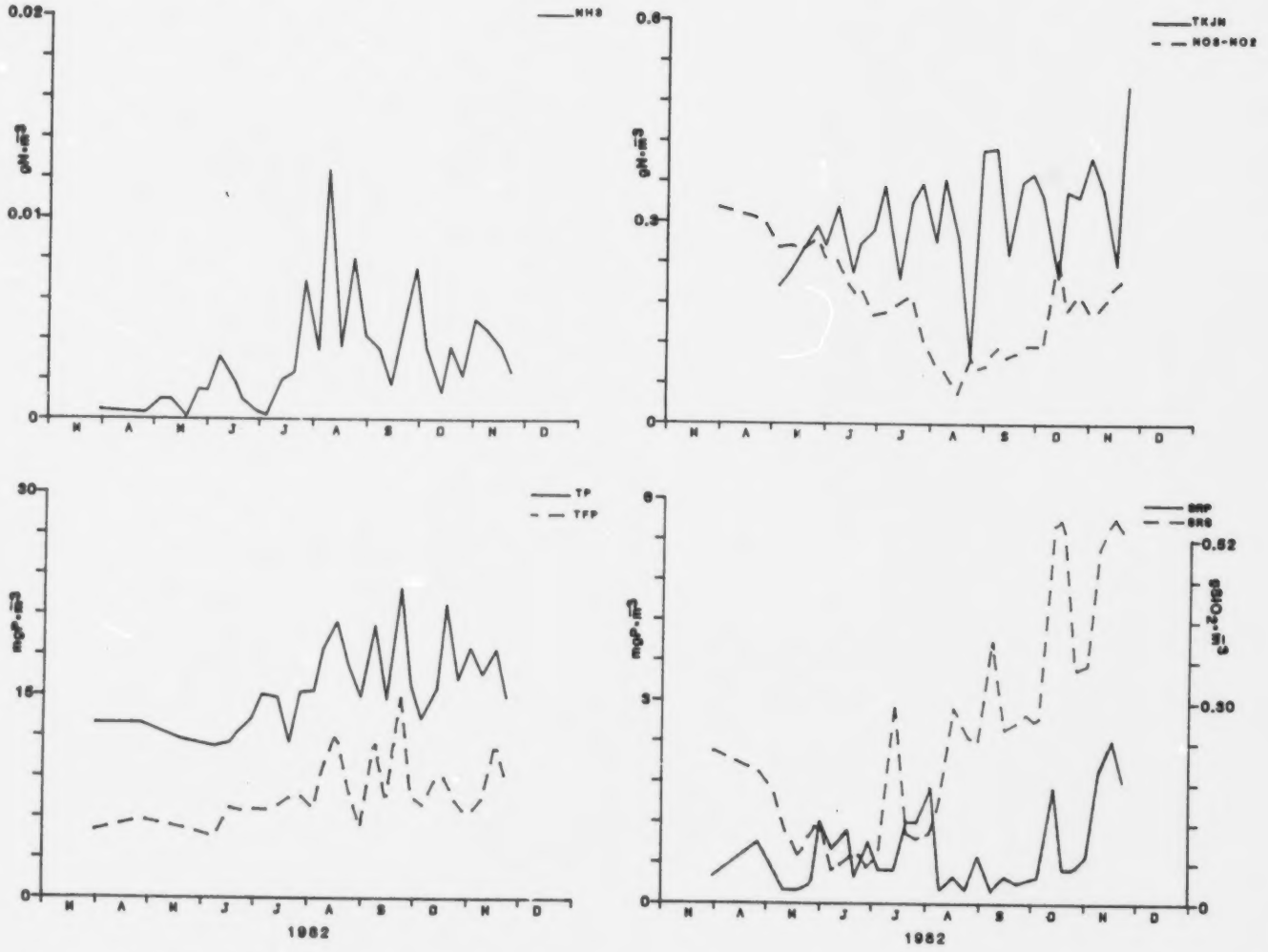


Figure 3b. (cont.)

Stn 93

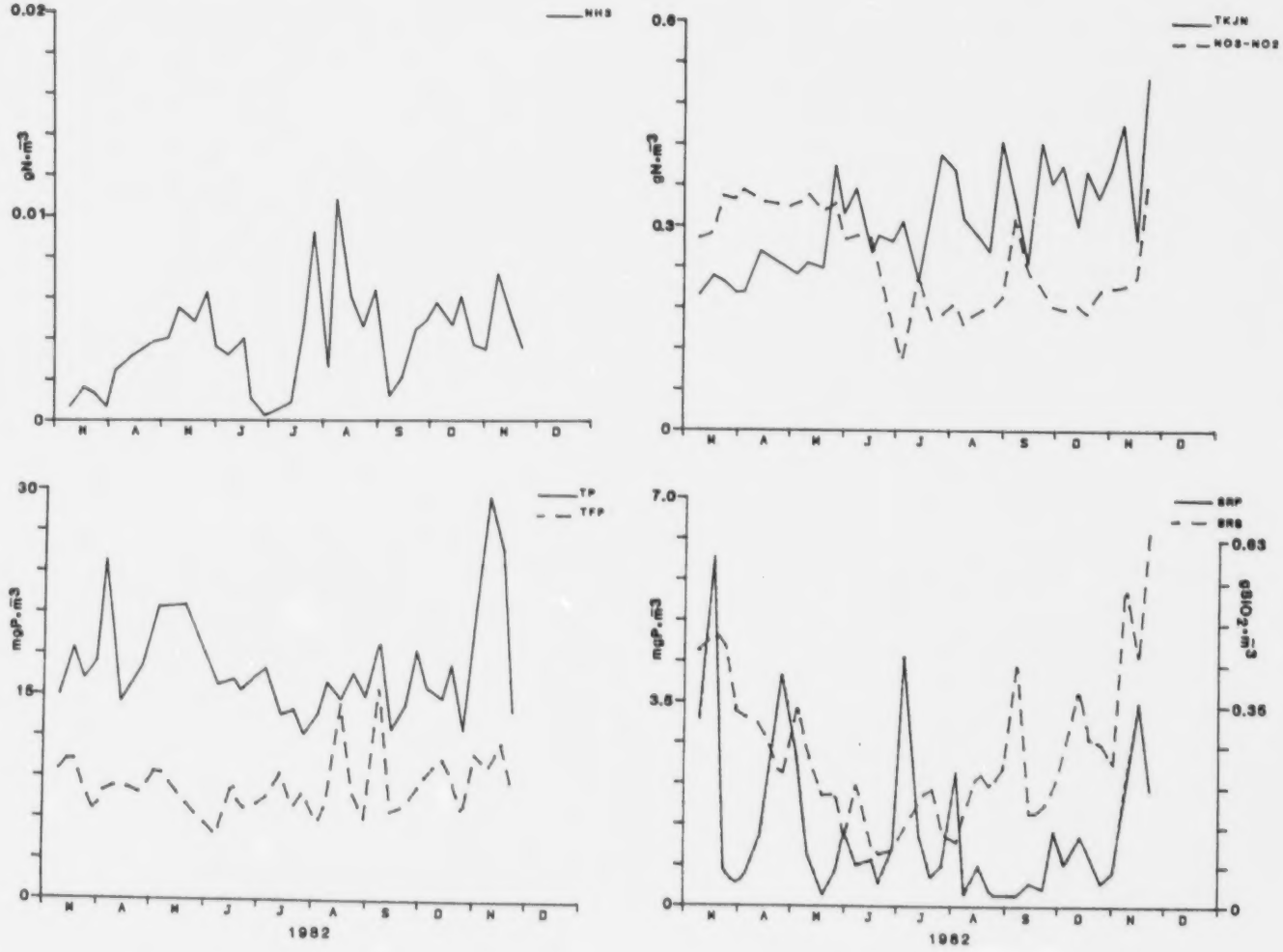


Figure 3b. (cont.)

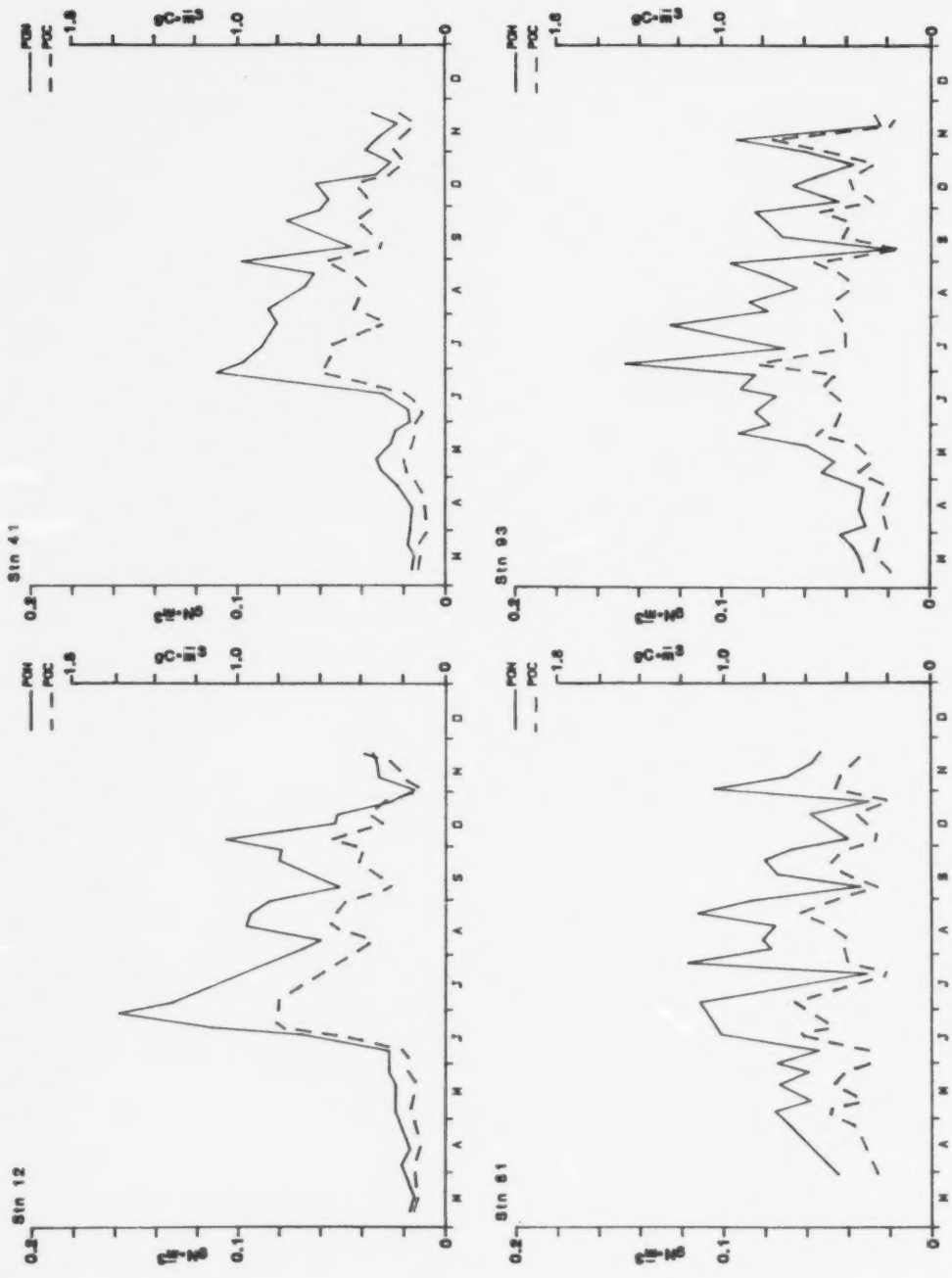


Figure 3b. (cont.)

Soluble reactive phosphorus and NO3NO2 reached minimum concentrations in the epilimnion later in the year than SRS. Like SRS, NO3NO2 had a definite pattern with high levels in autumn and spring. The maximum values ranged from 0.270 to 0.350 $gN.m^{-3}$ in 1981 and from 0.287 to 0.342 $gN.m^{-3}$ in 1982 (Table 3b). The lowest concentrations of NO3NO2 occurred in period three, but occasionally extended into periods four and two. They ranged from .059 to .135 $gN.m^{-3}$ in 1981, and from .102 to .170 $gN.m^{-3}$ in 1982. Since the seasonal pattern was consistent among stations, the significant station effect observed in the analysis of variance was due to the range in NO3NO2 levels observed among stations. Within each year, the concentrations could be ranked by their seasonally weighted means: station 12 equalled station 41 which was equal to or greater than station 93 which in turn was greater than station 81 (12=41>93>81). There was a 30 percent difference between the highest and lowest SWM station concentrations. There was also a significant difference between years: the seasonally weighted means were 10 to 17 percent lower in 1981 than in 1982. This decrease may reflect the shorter duration of period three in 1982. As a consequence, low values were present for a shorter period of the year in 1982, and the minimum levels reached during that period were not as marked. This would affect both a comparison between years within thermal periods and the seasonally weighted means. Perusal of the data confirms that the major difference between years occurred in period three.

Soluble reactive phosphorus was only measured in 1982. The values were extremely variable with many peaks in the spring and fall. However, relatively low values were always observed in late summer (Fig. 3b). There were some problems with the phosphorous analyses involving sporadic unknown

amounts of contamination from cap liners and filter interleaves, and delayed analytical analysis. Therefore the data provided only a rough seasonal pattern.

The second group of chemicals which increase to maximum levels in the summer consisted of TKJN and NH_3. Total Kjeldahl Nitrogen increased 19 to 46 percent in 1981 from minimum levels of 0.173 to 0.202 $gN.m^{-3}$ in the spring to maximum levels of 0.221 to 0.254 $gN.m^{-3}$ in thermal period three. In 1982 levels were higher initially than in 1981 and rose a further 36 to 57 percent from 0.215 to 0.228 $gN.m^{-3}$ in the spring to 0.341 to 0.364 $gN.m^{-3}$ in period 3 (Table 3b, Fig. 3a, 3b). The maximum generally occurred in period three, but on occasion extended into the second and fourth periods. These observed differences between years were significant. The seasonally weighted means in 1981 ranged from 0.199 to 0.220 $gN.m^{-3}$ while in 1982 they were higher, ranging from 0.273 to 0.310 $gN.m^{-3}$ (Table 3b).

Ammonia levels were very erratic. Seasonal patterns were not discernible at stations 41 and 93 in 1981 or at station 93 in 1982 (Fig. 3a, 3b). When distinct periods of maximum concentration were observed, they occurred in either period three or four (Table 3b). Levels of NH_3 differed between years and among stations (Table 4). In 1981 the seasonally weighted mean values were 0.012, 0.006, 0.010 and 0.020 $gN.m^{-3}$ at stations 12, 41, 81 and 93 respectively, while in 1982 they were 0.024, 0.021, 0.029 and 0.039 $gN.m^{-3}$ (Table 3b). The significant difference among stations may be due to the higher levels of NH_3 at station 93 and/or to differences in the seasonal pattern of NH_3 concentrations among stations.

The third group of chemicals, which showed no distinct seasonal trends, included TP and TFP. With such parameters it is best to consider only the seasonally weighted means. In 1981 the SWM TP levels for the four stations (12,41,81,93) were 0.015, 0.014, 0.014 and 0.016 $gP.m^{-3}$. In 1982 the SWM levels were 0.014, 0.013, 0.015 and 0.017 $gP.m^{-3}$ (Table 3b). There are significant differences among stations, but not between years (Table 4). The nearshore stations tended to have slightly higher TP concentrations. Total filtered phosphorous levels were not significantly different amongst stations, but did differ between years (Table 4). The seasonally weighted means were slightly higher in 1982: 0.0078, 0.0082 0.0073 and 0.0083 $gP.m^{-3}$ as compared with 0.0075, 0.0070, 0.0069 and 0.0066 $gP.m^{-3}$ for 1981 (Table 3b).

Biological Parameters

Six measures of biological activity were taken: SDW, DOC, POC, PON, CHLAU and CHLAC. Seston dry weight, particulate organic carbon, and particulate organic nitrogen are general measures of biomass which include both dead and living material. Since seston dry weight also includes mineralized material, the ash content (SIM) was determined and subtracted to calculate the organic dry weight (loss on ignition - LOI). Chlorophyll *a* corrected is a measure of living phytoplankton, and chlorophyll *a* uncorrected, is a measure of both living and partially decomposed phytoplankton. The difference between CHLAU and CHLAC, is a measure of the phaeophytin or the concentration of decomposing phyloplankton. In Lake Ontario phaeophytin has been related to zooplankton grazing (Glooshenko *et al.*, 1972). Changes in dissolved organic carbon

reflect dissolved carbon uptake by organisms and carbon production through decomposition and excess photosynthesis.

Season had a significant effect on DOC levels. However, one way analysis of variance applied within each station within each year indicated that the seasonal effect occurred regularly only at the mid-lake stations. Here DOC rose from 2.00 to 2.19 $gC.m^{-3}$ in the spring to maximum values of 2.32 to 2.59 $gC.m^{-3}$ in period three or occasionally period four (Table 3c). Seasonally weighted mean values ranged from 2.28 to 2.36 g $C.m^{-3}$ at the nearshore stations. In spite of the varying seasonal patterns no significant difference was detected among stations.

The seasonal patterns in SDW and LOI were similar at stations 12, 41 and 81. Maximum SDW concentrations occurred in thermal period three. Only at station 41 in 1982 did the maximum spread into periods two and four. The maximum LOI was usually synchronous with the maximum in SDW at these stations. The minimum levels of SDW and LOI occurred in periods one and five. At station 81, however, the lowest SDW could occur in other periods. Seston dry weight measurements include material resuspended from the bottom sediments, which has a higher proportion of mineral material than does living or freshly decomposing matter. The uncoupling of SDW and LOI at station 81 was presumably due to resuspension. Station 93 had totally different seasonal patterns in SDW and LOI. Resuspension is an important process at this station and the very high SDW concentrations in the spring and fall (periods one, four, and five) reflect this situation (Rosa 1985). Loss on ignition showed no consistent seasonal pattern but was less variable than at the other stations. Although similar seasonal patterns were observed in LOI and SDW,

the analysis of variance found significant seasonal effects only for LOI. The very different pattern in SDW at station 93 confounded the analysis of SDW. A three-way analysis of variance was run omitting station 93. Significant seasonal differences were detected in both variables, and there were no longer any significant differences amongst the stations. Maximum levels of both SDW and LOI were higher in 1981 than in 1982 (Table 4). Maximum SDW ranged from 2.545 to 2.950 $g.m^{-3}$ in the former year, to 1.850 to 2.600 $g.m^{3}$ in the latter at the three "normal" stations. The corresponding LOI levels ranged from 2.000 to 2.200 $g.m^{-3}$ in 1981, to 1.450 to 1.967 $g.m^{-3}$ in 1982. Although the maximum values were similar amongst these three stations, the minimum values varied from their lowest at station 41 (SDW-.460,.720 $g.m^{-3}$/LOI-.250, .533 $g.m^{3}$ in 1981 and 1982 respectively) to their highest at station 81 (SDW-1.483,1.500 $g.m^{-3}$/LOI-.933, 1.038 $g.m^{-3}$ in 1981 and 1982 respectively). At station 93 although the maximum and minimum SDW were greater than at any other station (6.050 and 2.400 $g.m^{-3}$ respectively), the range of LOI was similar (1.827 to 1.367 $g.m^{-3}$) indicating that most of the resuspended material was non-organic (Table 3c).

At the nearshore stations POC rose gradually in the spring from 0.267 to 0.500 $gC.m^{-3}$, while at the mid-lake stations POC rose later in the year, but more sharply from concentrations of 0.141 to 0.216 $gC.m^{-3}$. Maximum POC levels were observed in period two and ranged from 0.465 $gC.m^{-3}$ to 0.780 $gC.m^{-3}$. Levels remained high in period three (Table 3c). Significant differences did occur between years but were not observed among stations (Table 4). POC levels were 20 to 57 percent higher in 1981 than in 1982.

The trends in PON followed those in POC. Minimum values occurred in period one and ranged from 0.021 $gN.m^{-3}$ to 0.080 $gN.m^{-3}$. PON rose rapidly through the spring and peaked in period two at levels of 0.082 to 0.151 $gN.m^{-3}$. These high levels sometimes extended into period three, particularly in 1981 (Table 3c). The ratio of POC/PON varied between 6.1 to 6.7 in the spring, and decreased to 5.3 to 5.8 by mid-summer. It returned to spring levels raggedly through the autumn.

Chlorophyll a levels were variable and distinct seasonal patterns were not always observed (Fig. 3a). Seasonally weighted mean CHLAU concentrations ranged between 3.9 to 5.7 $mg.m^{-3}$. The levels differed significantly among stations, being highest at station 81 and lowest at station 41. Stations 93 and 12 had similar, though intermediate, CHLAU levels.

Corrected chlorophyll a levels also showed little seasonal pattern (Fig. 3a). Phaeophytins, however, increased in the later thermal periods. In the spring only 3.5 to 9.0 percent of the total chlorophyll was composed of phaeophytins. In period three the percentage rose to 10.3 to 14.4 percent and continued to increase slowly through the autumn until levels of 10.5 to 19.1 percent were observed in period five.

The relationships amongst these biological measures were examined by calculating correlation coefficients first for the entire data set, and then for each thermal period within each year. The overall correlations between CHLAU and CHLAC and between POC and PON were high, 0.9700 and 0.9438 respectively (Table 5). However, the overall correlations between these two groups and between them and LOI were always less than 0.6100. When the correlations were examined across the year, the relationship between CHLAU and

TABLE 5: Seasonal relationships between general biological parameters determined by Pearson's Correlation Coefficient. Number of samples >20. There was insufficient data for Period V.

			Seasonal Period			
Year	Measure	Total	I	II	III	IV
1981	ICHLA-U/IPOC	0.5923	0.7582	0.8159	0.4468	0.3425
1981	ICHLA-C/IPOC	0.5763	0.7456	0.8128	0.4127	0.2691
1981	ICHLA-U/IPON	0.6052	0.7482	0.9008	0.5143	0.4967
1981	ICHLA-C/IPON	0.5792	0.7329	0.8902	0.4856	0.4237
1981	ICHLA-U/ICHLA-C	0.9700	0.9974	0.9980	0.9755	0.9228
1981	IPOC/IPON	0.9438	0.9699	0.9434	0.8354	0.7960
1982			0.9616	0.8644	0.7730	0.8799
1981	LOI/ICHLA-U	0.4954	0.7283	0.1104	0.4247	0.5075
1981	LOI/ICHLA-C	0.4843	0.6657	0.1866	0.4598	0.5078
1981	LOI/IPOC	0.6146	0.7832	0.9560	0.7344	0.5288
1982			0.7704	0.7245	0.5169	0.0645
1981	LOI/IPON	0.6205	0.8250	0.9621	0.7700	0.4881
1982			0.8788	0.7094	0.4586	0.0368

TABLE 6: The relationships between total algal biomass and other biological parameters, as determined by Pearson's Correlation Coefficient. Number of samples >20.

			Seasonal Period				
Year	Measure	Total	I	II	III	IV	V
1981	IPOC	0.4430	0.7868	0.0808	0.3498	0.5808	--
1982			0.7128	0.3604	0.3321	0.2928	--
1981	IPON	0.4142	0.7667	0.0922	0.5288	0.5272	--
1982			0.7685	0.1100	0.0052	0.3235	0.5913
1981	ICHLA-U	0.5461	0.8696	0.2658	0.8320	0.1897	--
1981	ICHLA-C	0.5578	0.8667	0.2651	0.8397	0.0734	--
1981	DRY WT.	0.2757	0.2301	0.2723	0.2240	0.8515	--
1982			0.1570	0.2552	0.3309	0.3104	--
1981	LOI	0.2429	0.3679	-0.6255	0.3548	0.4064	--
1982			0.5665	0.3231	0.3383	0.2730	--

NOTE: -- indicates insufficient data

CHLAC remained high until period four, when it dropped slightly to 0.9228, presumably due to the increasing amount of phaeophytin in the system. The relationship between POC and PON decreased steadily through the year. The seasonal correlations between the two groups were moderate in period one (0.7329 to 0.7582), improved in period two (0.8159 to 0.9008), and nonexistent in periods three and four. Loss on ignition was more closely correlated with POC and PON than with chlorophyll. But again the relationship deteriorated in the latter part of the year (Table 5). The decreased correlation of PON with LOI as the season progressed suggests a periodic or irregular accumulation of refractory organic material through the year.

In comparing the chemical measures of biological communities with total phytoplankton biomass, very poor overall correlations were found (Table 6). Seasonally, the correlations were best in period one: those with chlorophyll a were slightly better than those with POC or PON and those with SDW and LOI were poor (0.1570 to 0.5775). For the remainder of the year the relationships between total algal biomass and POC, PON, SDW and LOI were non-existent. Algal carbon, however, comprises only a small proportion of the POC pool (Fig. 4) which is also represented by SDW and LOI. These measures will only be closely correlated with algal biomass when algal carbon changes in step with the other carbon components. The relationship between total algal biomass and chlorophyll a was erratic, being bad in periods two and four, and good in periods one and three. Algal biomass should have a closer relationship with chlorophyll a than with POC. The chlorophyll a content of cells, however, is dependent on several factors: light intensity, mixed

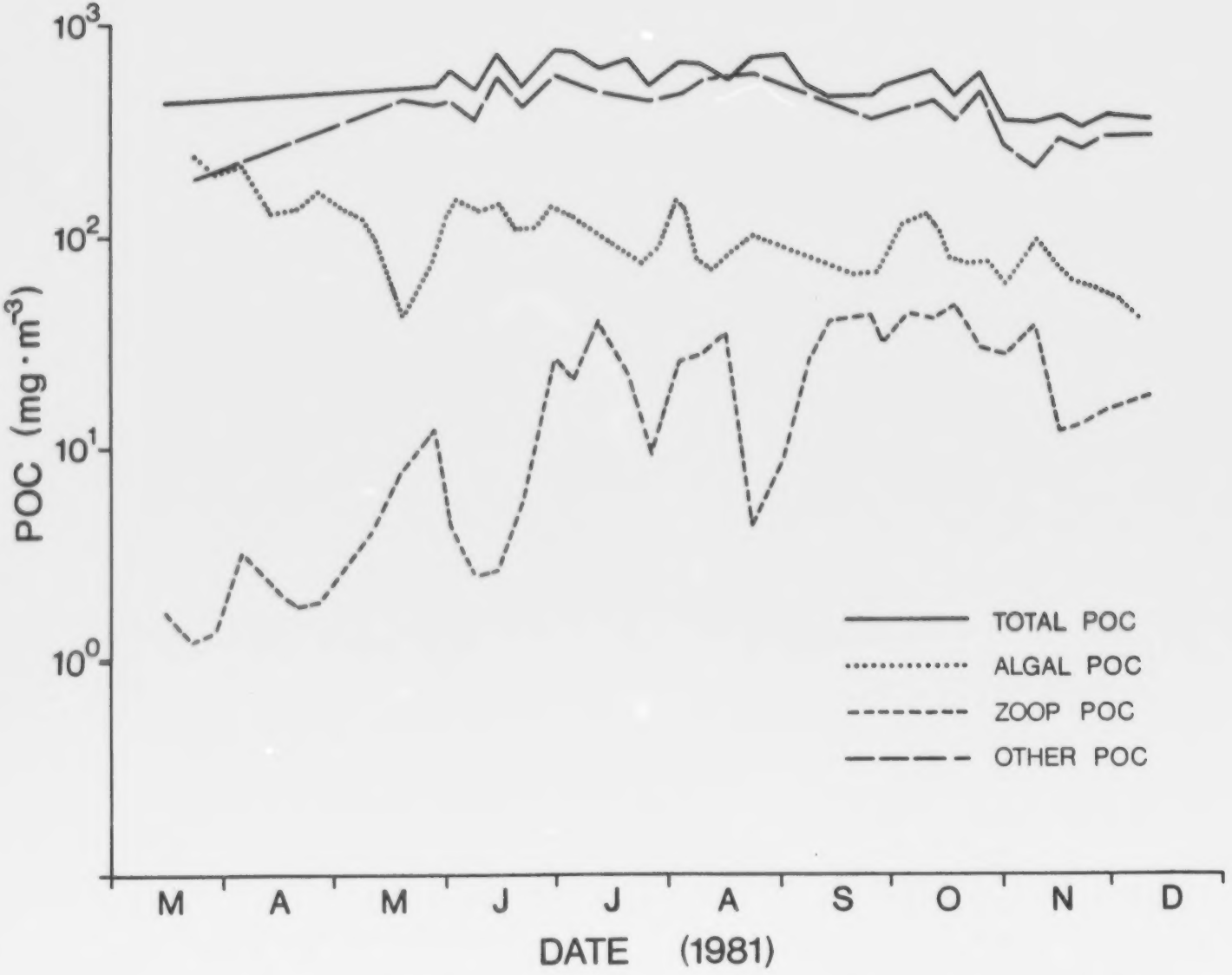


Figure 4. Seasonal breakdown of particulate organic carbon into its algal, zooplankton, and other, fractions: Station 81, 1981.

depth, nutrients and algal class. When several of these factors are changing simultaneously the relationship will change and the overall correlation deteriorate. In addition, the measurements of both algal biomass and chlorophyll a contain a large amount of variability, thereby further reducing the likelihood of strong correlation. Again there were insufficient data to calculate correlations for period five.

The relationships amongst the stronger biological parameters (algal biomass, CHLAC, POC, and PON) and important environmental variables were examined using stepwise multiple regression. The analyses were broken down on the basis of station location and season. The seasons were grouped as spring (periods one and two), summer (period three), and fall (periods four and five). The stations were divided into mid-lake (12,41), nearshore-eastern basin (81), and extreme nearshore (93). Better results were obtained when 81 and 93 were separated. For the summer period the data from all stations were grouped to obtain a sufficient sample size. The environmental variables included the major nutrients (SRS, TFP, NO3NO2), and physical parameters (EBT, EU, DM, DZ/DM, and irradiance) important to phytoplankton.

In some analyses depth and light measures were replaced by a composite index developed by Riley (1957) to characterize the light environment of phytoplankton. This index, known as the effective light regime (ELR) (Ramberg 1979), is calculated as follows:

$$Ip = 0.45\ Io$$

$$ELR = \frac{Ip(1-e^{-K \cdot DM})}{K \cdot DM}$$

where Io = insulation

Ip = photosynthetically available light (see Stadelmann, et al., 1974)

K = extinction coefficient

Irradiance data were provided by the National Water Research Institute and were collected on the roof of the Canada Centre for Inland Waters, at the western end of Lake Ontario.

The phosphorous pool available for algal growth cannot be measured directly. Scavia's (1979) ecological model of Lake Ontario phytoplankton and phosphorous dynamics suggests that much of the TFP pool is available to the phytoplankton during the spring and autumn, but not during the summer when SRP is a more accurate measure. Unfortunately, the lack of 1981 SRP data and the relatively short length of period three in 1982 reduced the summer sample size below acceptable levels. Accordingly TFP was used to represent the phosphorous pool at all times.

The observed biological community is the result of both present and past environmental conditions. In order to incorporate this temporal dimension the environmental variables were lagged by zero to three weeks and correlated with the biological parameters. Only the lags with the greatest correlation within each variable were entered in the analysis.

For each biological measure, different environmental variables were important depending on station location (Table 7). Clearly, the various regions of the lake need to be examined independently. For this reason, although some statistically significant relationships were found in the summer data, the data from all stations, when grouped, should be regarded with caution, and are not considered in the text.

The environmental variables were best able to account for variations in biological parameters in the spring, and in the mid-lake as compared with the

TABLE 7: Associations amongst the biological and environmental variables as determined by stepwise linear regression. Bracketted numbers indicate the lag period, in weeks.

	Spring (periods 1 & 2)					Summer (period 3)*					Autumn (periods 4 & 5)				
Total Algal Biomass	F	D.F.	Sig.	Variable	SUM%**	F	D.F.	Sig.	Variable	SUM%	F	D.F.	Sig.	Variable	SUM%
Stations 12,41	60.82	2,47	0.000	EBT	58.5	9.18	3,41	0.000	SRS	17.6	18.86	3,37	0.000	DM	35.6
				TFP	72.1				EBT(-2)	26.9				ELR	47.4
									NO_3NO_2	40.2				TFP	60.5
81	9.60	1,22	0.001	SRS(-3)	45.7						13.46	3,13	0.000	EBT(-3)	50.9
														DZ/DM(-2)	67.9
														TFP(-3)	75.7
93	7.71	2,21	0.003	SRS(-1)	29.8						-	-	n.s.	-	-
				ELR	42.3										
Chlorophyll a (c)															
Stations 12,41	21.41	3,31	0.000	NO_3NO_2	56.4	14.21	3,30	0.000	DZ/DM	37.2	8.26	2,26	0.002	SRS	14.7
				DZ/DM(-3)	62.7				NO_3NO_2	49.3				IRRAD(-1)	38.9
				SRS	67.5				TFP	58.7					
81	7.90	1,13	0.015	SRS(-3)	37.8						-	-	n.s.	-	-
93	18.99	2,16	0.000	SRS(-1)	42.4						8.29	1,10	0.016	NO_3NO_2	45.3
				NO_3NO_2		70.4									
Particulate Organic Carbon															
Stations 12,41	94.70	2,44	0.000	NO_3NO_2	78.9	6.52	2,32	0.000	ELR(-3)	15.8	23.04	2,38	0.000	DM	46.5
				DZ/DM(-2)	81.1				SRS(-2)	28.3				TFP	54.8
81	21.21	1,24	0.000	NO_3NO_2	46.9						18.95	1,17	0.000	SRS(-3)	52.7
93	20.35	2,22	0.000	SRS(-2)	50.0						-	-	n.s.	-	-
				NO_3NO_2		64.9									
Particulate Organic Nitrogen															
Stations 12,41	149.48	2,44	0.000	EBT	82.4						36.22	2,38	0.000	EBT	54.2
				ELR(-2)	87.2									TFP	65.6
81	21.35	2,17	0.000	TFP	48.5						-	-	n.s.	-	-
				SRS(-3)	71.5										
93	18.74	2,22	0.000	SRS(-2)	44.5						-	-	n.s.	-	-
				NO_3NO_2		63.0									

* due to the small sample size all stations were grouped - results should therefore be taken cautiously.

** SUM% = accumulative percent of explained variance.

nearshore regions (Table 7). In the mid-lake 72.1 percent and 60.5 percent of the variation in total algal biomass could be accounted for in spring and fall respectively; in the nearshore the values were 42.3 and 45.7 percent for stations 93 and 81 in the spring respectively, and a non-significant percent and 75.7 percent in the fall. Total filtered phosphorus, EBT (spring only), and light-depth variables (DM,ELR:autumn only) described the mid-lake variation in algal biomass. Nearshore, SRS and ELR (93 only) were important in the spring, while, like the mid-lake stations, EBT, TFP and DZ/DM were important in the fall at station 81. In the autumn, total algal biomass could not be predicted at station 93.

A different set of variables were associated with CHLAC. Soluble reactive silica and NO_3NO_2 were often important both mid-lake and nearshore, in both spring and fall. Mid-lake, the light regime was also critical: DZ/DM(-3) in the spring, and IRRAD(-1) in the autumn. In the spring, 37.8 to 70.4 percent of the variation in CHLAC could be explained, but only 38.9 to 45.3 percent in the fall.

Predictive equations for POC, and particularly PON, were slightly better than those for algal biomass and CHLAC (Table 7). The accumulated percent of explained variance for POC ranged from 46.9 to 81.1 percent in the spring and n.s. to 54.8 percent in the fall. Similar figures for PON were 63.0 to 87.2 percent and n.s. to 65.6 percent. Like CHLAC, POC in the spring was always related to SRS and NO_3NO_2 nearshore, and NO_3NO_2 and DZ/DM(-2) mid-lake. In the autumn DM and TFP were important mid-lake. Particulate organic nitrogen responded more like total algal biomass. Mid-lake PON was associated with EBT, TFP and a light-depth variable (ELR-2). In the spring,

nearshore, SRS, TFP and NO_3NO_2 were important. None of the environmental variables could account for autumnal changes in either POC at station 93 or in PON in the nearshore.

SAMPLING STRATEGY

Two areas of sampling design were analyzed: the adequacy of discrete depth samples to describe epilimnion conditions, and the relationship of sampling frequency to variability in estimates of seasonally weighted means. This variability, in turn, is directly related to the accuracy with which the sampling frequency describes the seasonal pattern. These are two very different topics and will be dealt with separately.

Sample Type

Particulate organic carbon, PON and chlorophyll a were measured in the epilimnion in both discrete depth and integrated samples. During isothermal conditions samples were collected from 1, 10, 25 and 0 to 20 m; under stratified conditions, from 1 m, 1 m above the thermocline and from 0 to 1 m above the thermocline or 0 to 20 m whichever was less. The effectiveness of 1 m and two- to three-point depth-weighted-average (DWA) discrete depth samples, in describing epilimnetic concentrations, was determined by comparing them with the integrated samples. The different types of samples were positively correlated and therefore compared using a paired t-test. Significant differences amongst all three sampling methods were found for POC and PON in 1981. The chlorophyll concentrations that year were significantly different between 1 m and integrated, and between 1 m and DWA samples, but not between the DWA and integrated samples (Table 8). To determine if the

TABLE 8: A paired t-test comparison of biological measures, estimated by discrete depth samples, converted to depth-weighted average epilimnetic values (DWA), integrated water samples (INT), and 1 m discrete depth samples (1M) calculated over the entire season and within the seasonal-thermal periods.

Measure	Comparison	Yr.	Total	I	II	III	IV	V
POC								
	1M-DWA	81	0.000***	0.025*	0.031*	0.009**	0.025*	-
		82	0.332	0.867	0.227	0.167	0.331	-
	1M-INT	81	0.000***	0.025*	0.058	0.009**	0.046*	-
		82	0.335	0.406	0.131	0.467	0.333	-
	DWA-INT	81	0.000***	0.822	0.062	0.008**	0.096	-
		82	0.993	0.183	0.881	0.875	0.966	0.883
PON								
	1M-DWA	81	0.000***	0.025*	0.022*	0.017*	0.025*	-
		82	0.103	0.825	0.150	0.458	0.136	-
	1M-INT	81	0.000***	0.025*	0.043*	0.017*	0.046*	-
		82	0.822	0.486	0.957	0.779	0.686	-
	DWA-INT	81	0.042*	0.036*	0.105	0.342	0.008**	-
		82	0.402	0.077	0.818	0.259	0.755	0.430
CHLA-U								
	1M-DWA	81	0.019*	0.134	0.172	0.159	0.323	-
	1M-INT	81	0.021*	0.089	0.161	0.168	0.356	-
	DWA-INT	81	0.876	0.152	0.063	0.789	0.958	-
CHLA-C								
	1M-DWA	81	0.036*	0.102	0.175	0.291	0.340	-
	1M-INT	81	0.000***	0.297	0.161	0.185	0.355	-
	DWA-INT	81	0.491	0.120	0.143	0.858	0.510	-

NOTE: All correlations between integrated and calculated variables were positive.
Significance: * < 0.05, ** < 0.01, *** < 0.001

disparities were more characteristic of one period of the year than another, paired t-tests were performed in each thermal period (Table 8). The differences observed for chlorophyll were not associated with any particular season and were only significant when the whole year was compared. With respect to POC and PON, the 1 m values were always significantly different from the DWA and integrated estimates. The DWA and integrated concentrations were more similar. Particulate organic nitrogen DWA estimates were significantly different in periods one and four, while POC estimates were different in period three. However the probability was less than 0.1 that the two methods were sampling the same POC 'population' in periods two, four, and five. This indicates that the POC vertical dispersion was patchy and not well estimated even by depth weighted averages for most of 1981. The paired t-tests found no significant differences resulting from the three sampling methods or any parameter in 1982.

Sampling Frequency

Using the background data of weekly sampling, the physical, chemical and biological data were re-analyzed assuming sampling intervals of 2, 3, 4, 5 and 6 weeks. Seasonally weighted mean values were determined for each parameter and compared with that from weekly sampling. Where data values were missing, the next closest date was substituted. Thus, the changes observed may be slightly inflated. The percent deviations from the one week value were plotted against the proportionate sampling frequency (Fig. 5). These graphs illustrate the potential range of the estimates at different sampling frequencies, given that the estimate at one week is the true mean. Some

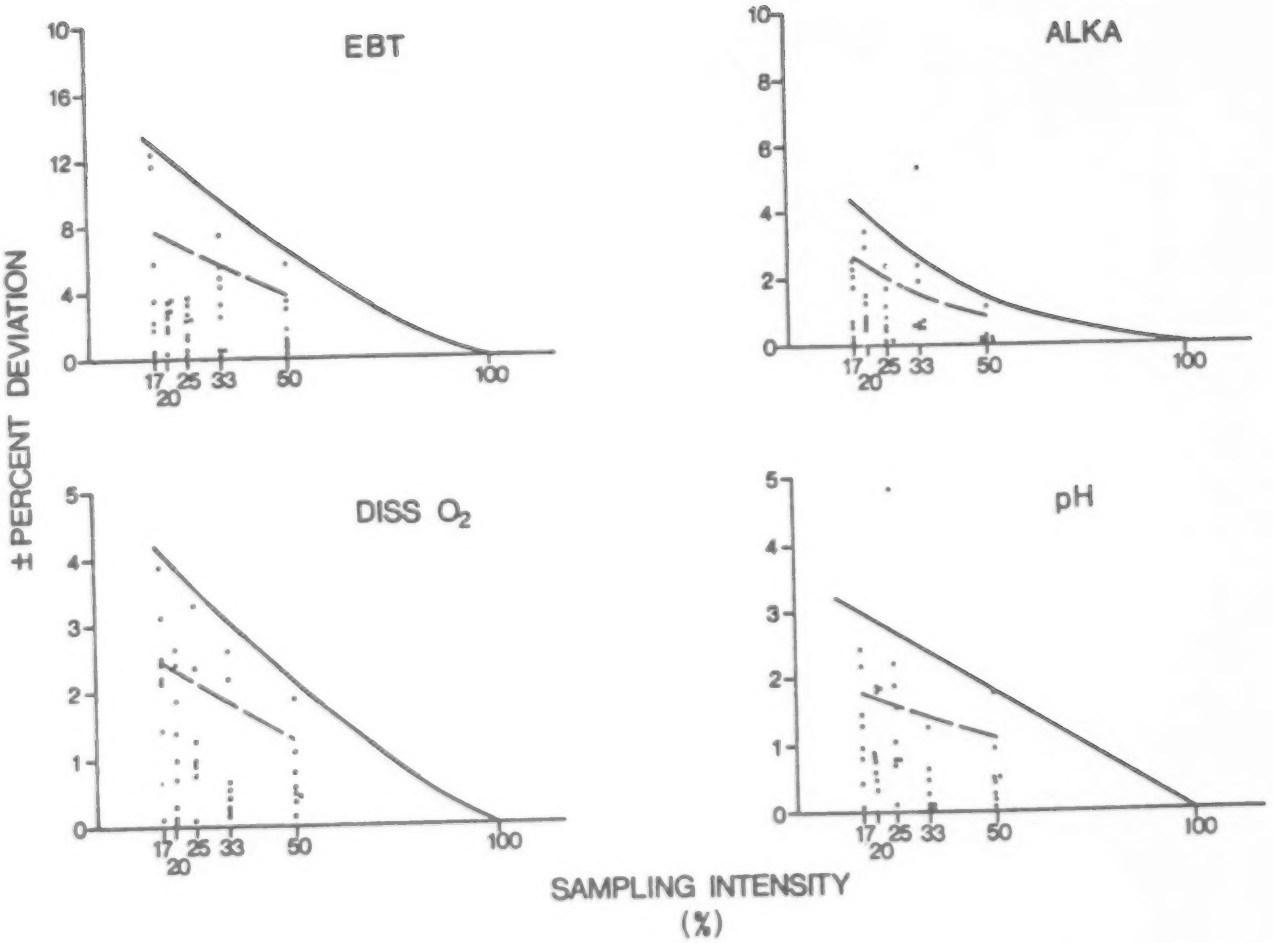
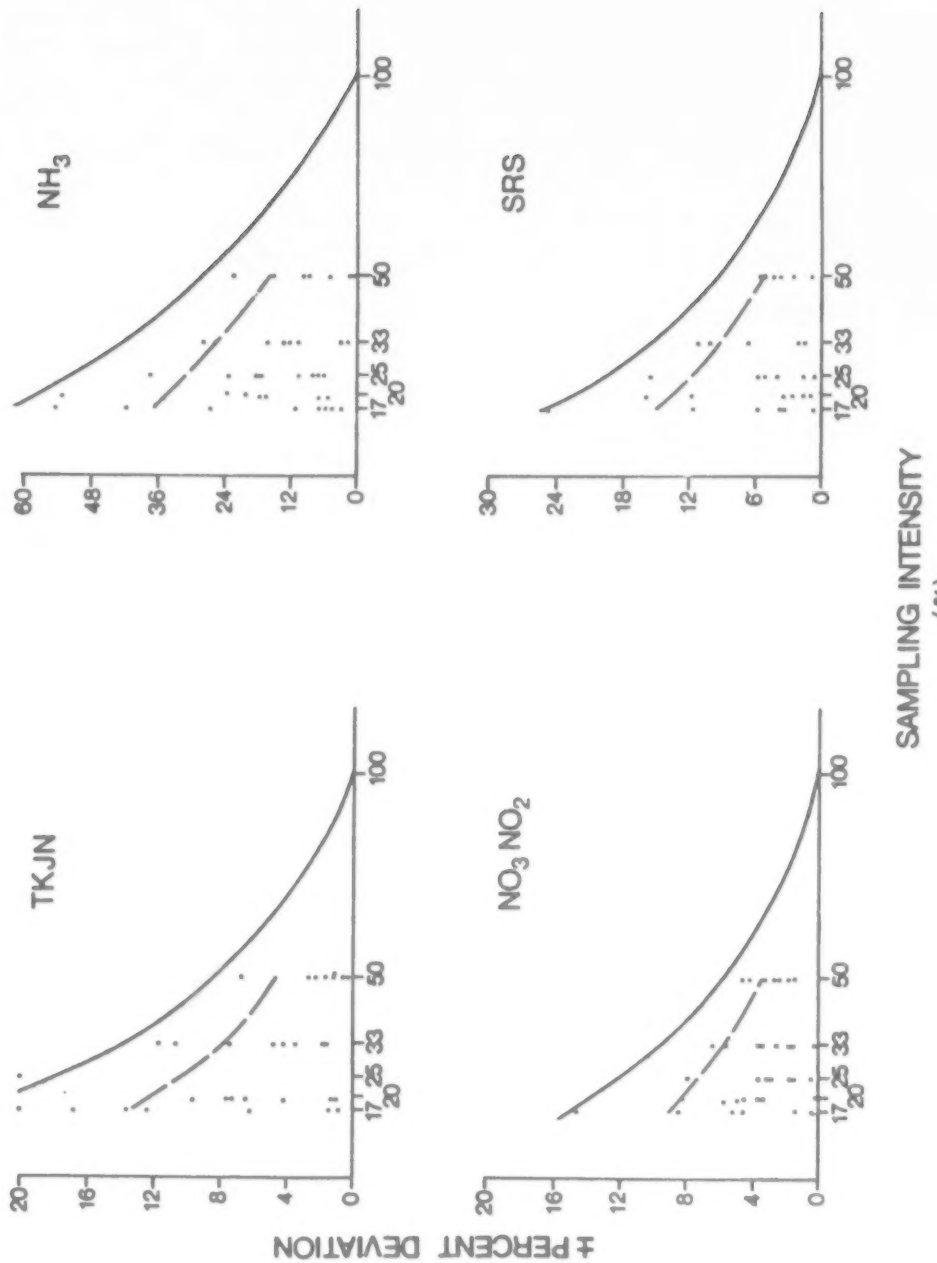


Figure 5. The effect of decreasing sampling frequency on the distribution of the estimates of the seasonally weighted means of biological ,nutrient, and physical parameters. The solid line depicts the range of dispersion; the dashed line, the boundary below which two thirds of the points fell.



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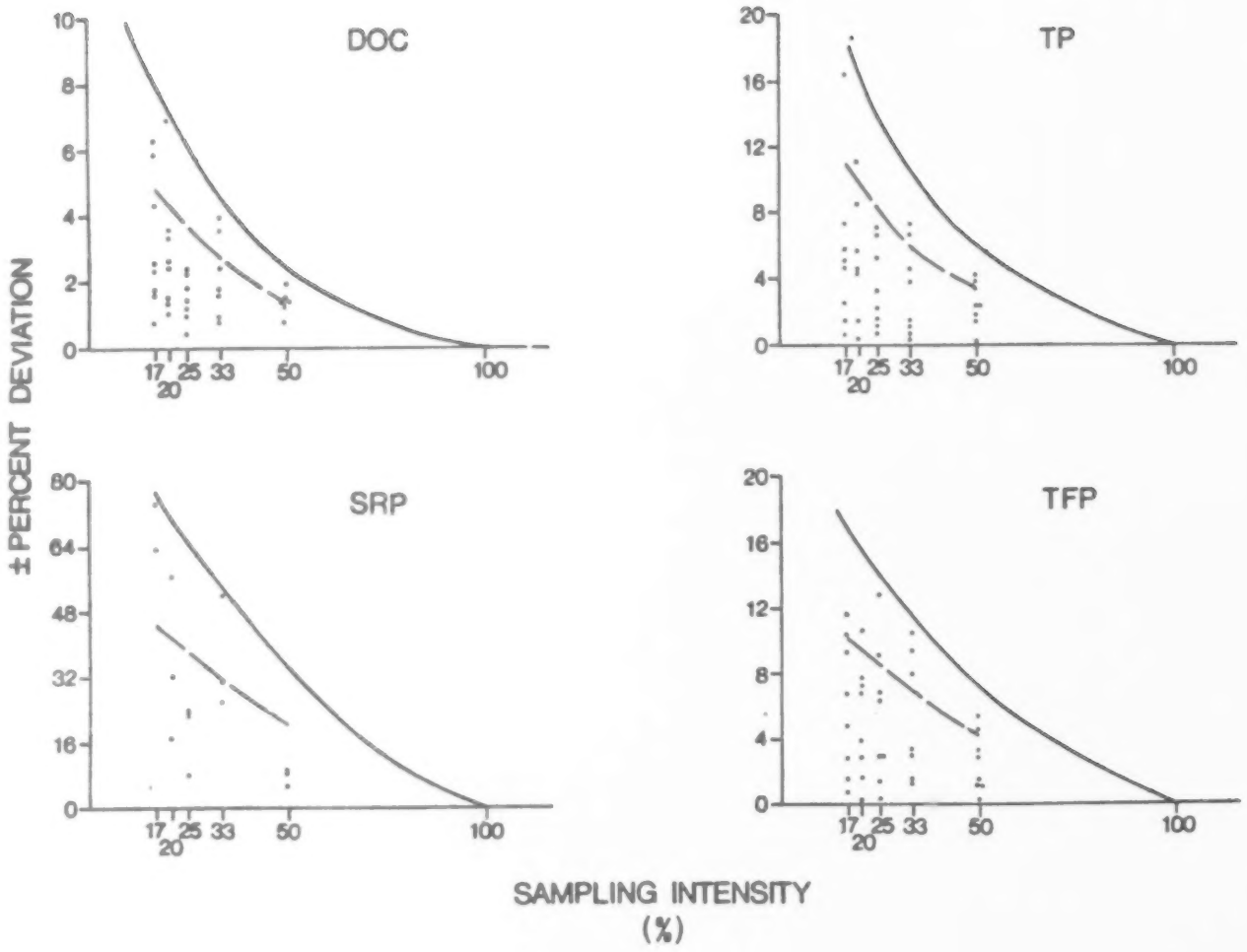

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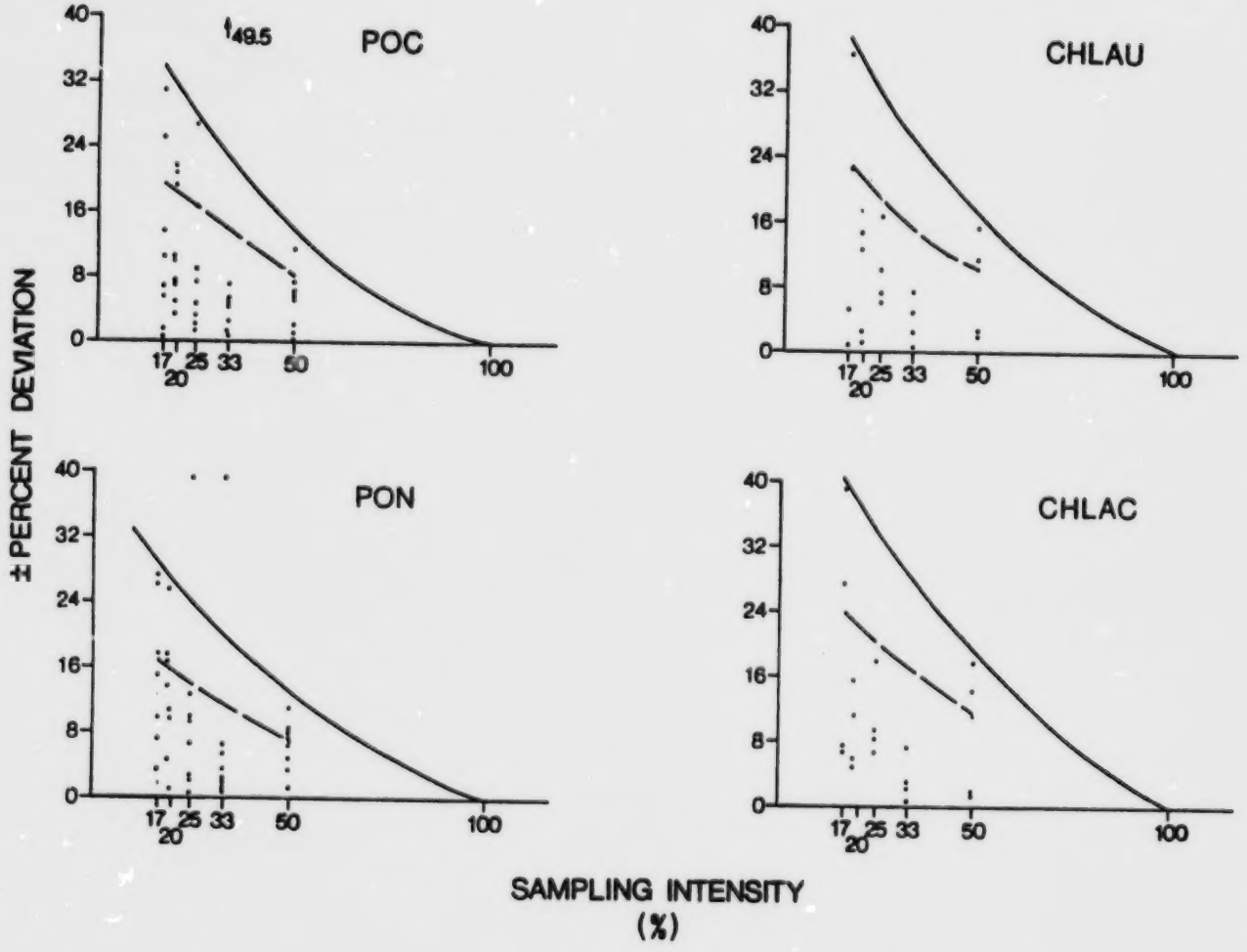

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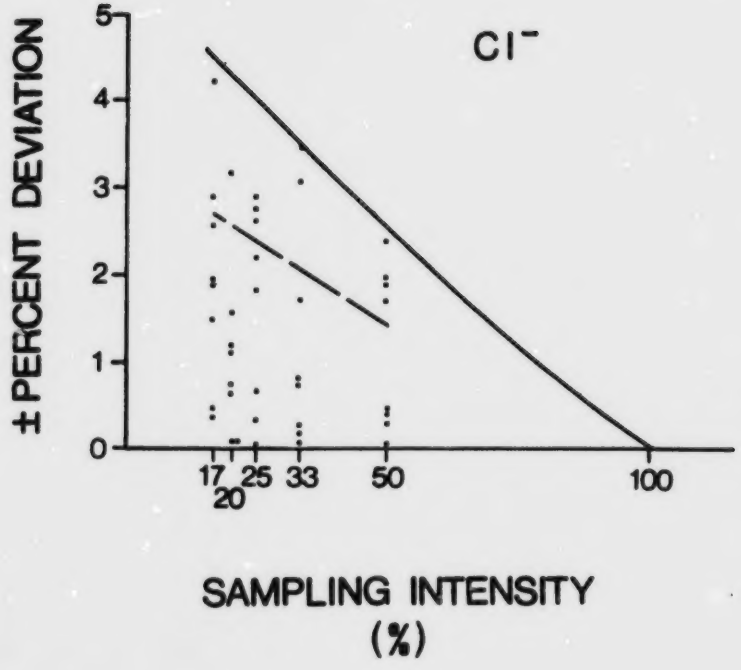


Figure 5. Continued

parameters show very little change, even with long sampling intervals; these are the physical variables: ALKA, pH, $DISSO_2$ and CL. The accuracy of the estimate of the seasonally weighted mean of the next set of parameters increased moderately with decreased sampling interval. The range was less than $\pm$ 10 percent with biweekly sampling and between $\pm$ 11 to 20 percent with a monthly (four weeks) sampling interval. Most of the nutrient parameters SRS, NO3NO2, TKJN, TFP, and TP and temperature fell in this category. Members of the third group of parameters can change very rapidly and do not have smooth seasonal patterns. As sampling interval increases, the accuracy of the estimate of their seasonally weighted means decreases rapidly. These variables include the biologically related parameters, POC, PON, CHLAU and CHLAC, as well as two nutrients, SRP and NH_3. With biweekly sampling, the range is $\pm$ 13 to 19 percent for POC, PON, CHLAU and CHLAC, and $\pm$ 27 to 32 percent for SRP and NH_3. With monthly (four weeks) sampling these estimates increase to $\pm$ 27 to 34 percent for the biological parameters group and $\pm$ 42 to 64 percent for the nutrient parameters.

DISCUSSION

INTERACTION OF BIOLOGICAL AND CHEMICAL VARIABLES

In 1972 a major study of processes operating in Lake Ontario was undertaken jointly by the American and Canadian groups studying the Great Lakes. Several models depicting phytoplankton dynamics were developed using this data base (Simons 1976, Scavia 1979). Simons' model compartmentalized the lake into 4 vertical layers and 21 zones to study the effects of vertical

and horizontal transport processes on phytoplankton dynamics. Predictions of phytoplankton density were made in the absence and presence of transport and compared with the observed data. Scavia's model considered only a vertical ecosystem, and aimed at describing the interactions of the various components of the biological community with themselves, major nutrients (P,N,Si), and physical variables (light, temperature, vertical mixing). In this model algal production was a temperature dependent variable limited by light or nutrients. He found light to be the limiting factor in spring, until early June when the water warmed suddenly as stratification developed, and again in autumn, as of mid-September. In the summer the algae were phosphorus limited. Sridharan and Lee (1977) suggested that nitrogen could also be limiting in the late summer. Although phytoplankton production was high in summer in Scavia's model, particularly in August and September, zooplankton grazing was also severe and there was little net change in phytoplankton standing crop.

The mid-lake phytoplankton communities in 1981 and 1982 show similar patterns of response to these environmental variables as predicted by Scavia's model (Table 7). Scavia suggested that light was the limiting factor, in the spring, while regression analyses showed total algal biomass was most closely correlated with EBT and TFP. This difference is probably the result of differences in the time scale considered. Temperature changes very slowly in early spring and only starts to rise steeply in early June, at which time light ceases to be limiting. The present analysis groups all data from the early spring to well developed stratification and temperatures of 16.9°C. As stratification develops there is a burst of phytoplankton growth which

explains the strong correlation between algal biomass and temperature observed in the present study. Scavia indicated that phosphorus was limiting in the summer. Clearly some of the phosphorous limitation was included in the spring period in the present study. The present study agrees that light is the principal limiting factor in the autumn since the effective light regime and mixed depth are important correlates of algal biomass. Phosphorous levels at this time, however, also appear to play a role in algal dynamics. If CHLAC is taken as the measure of algal biomass for comparison with Scavia's model, it supports the importance of light in algal dynamics in the spring as well as in the fall. However, the primary correlate is NO3NO2. It is unlikely NO3NO2 controls production because it has never been found limiting at this time of year in the past and has been increasing in concentration in the lake at a rate of 9.5 $mg.m^{-3}.yr^{-1}$ since 1969 (Stevens and Neilson, in prep.). Since nitrate is the primary N source for phytoplankton growth (Wetzel 1975), changes in NO3NO2 may reflect phytoplankton uptake and production, especially before degradation processes increase the importance of cycling ammonia. This would explain the correlation of NO3NO2 with CHLAC, particularly in the spring. Interestingly, SRS is also important in predicting CHLAC. In the nearshore neither algal biomass nor CHLAC showed a consistent relationship with light. Only at station 93, where resuspension of bottom sediments is pronounced in the spring, did ELR become important. Soluble reactive silica was the principal correlate. Major diatom blooms inshore in the spring sharply deplete silica levels and a lack of SRS may limit further diatom blooms. Phosphorous levels have also been driven very low by this time (Johannsson et al., 1985). It may be a combination of these two nutrient

levels that are limiting diatom growth. When silica concentrations are low, diatoms are no longer as efficient at taking up phosphorus (Tarapchak, pers. comm.) and therefore both nutrients may become limiting. This is an extension of the Schelske and Stoermer (1972) hypothesis of algal succession which suggests that diatoms can compete for phosphorus more effectively than greens and blue greens but do not dominate under low phosphorous conditions in the summer because they have become silica limited. The ability of the nutrient and environmental variables to predict algal biomass and CHLAC was greater in the spring then the fall.

The spring is a period dominated by growth, and all the variables considered in the analyses affect the production aspect of population dynamics. Consequently, when growth is the prominent force, population size can be more readily explained.

The accounting of 67 to 72 percent of the spring variation in the mid-lake is respectable because neither algal biomass nor CHLAC are exact measures. However, in the fall, only 38.9 to 60.5 percent of variation could be explained.

During the summer and autumn, loss factors such as sedimentation and zooplankton grazing, become much more important population processes (cf. Reynolds 1984, Lehman et al. 1975). These processes were incorporated into Scavia's model for Lake Ontario and were important at these times (Scavia 1979, Fig. 3). This change in emphasis in population processes reduces the ability of growth factors to predict algal standing crop. The inclusion of mixed depth in the analysis, as a surrogate for sinking losses, did improve the predictability of algal biomass in the fall. Similarly, the inclusion of some measure of grazing pressure may further improve predictability. Simons

(1976) demonstrated that while vertical mixing was the predominant physical force in the spring, horizontal transport was prevalent in the fall. Therefore, predictability in the autumn will never be as accurate as in the spring.

All the models deal with whole-lake or open-water phytoplankton dynamics. The present analysis suggests that the mid-lake situation is more predictable than the nearshore. This again may be due to a greater importance of loss factors nearshore, but also, undoubtedly, is the result of the more pronounced and frequent physical disruptions, such as resuspension and horizontal translocation which disturb the continuity of the data.

Particulate organic carbon and PON are surrogates for the whole pelagic community: most is contributed by sources other than macrozooplankton and algal biomass (Fig. 4). These could come from detrital, colloidal and microzooplankton sources. Spring is a time of growth, not only for the phytoplankton, but for the entire community. Particulate organic carbon and nitrogen reach their greatest levels in thermal periods two and sometimes three. During the spring, NO3NO2 was important in predicting POC at all stations and PON at station 93. Presumably NO3NO2 changes are an integral measure of phytoplankton production, as mentioned above, and thus the energy base for community growth. In the mid-lake, DZ/DM accounts for a small additional proportion of the variance. The levels of PON are more closely tied to algal biomass than are those of POC. Temperature is the primary correlate with PON, as with total algal biomass, but, like POC, a light-depth parameter has a minor secondary role mid-lake. In the autumn, loss factors again become more important: mixed depth was the principal predictive

factor of POC in the mid-lake. The effect could be due to dilution of epilimnetic POC by lower hypolimnetic levels and/or to sedimentation. The greater effect of loss factors in autumnal PON was only reflected in the lower explained variance.

A consistent relationship exists between SRS and all biological parameters in the nearshore in the spring. This suggests that silica may become limiting nearshore and that events in the phytoplankton community are mirrored in the whole community as described by POC and PON.

Multiple linear regression of biological and environmental variables has proven effective in delineating important associations as confirmed by previous models. The technique as applied to the Bioindex data could be greatly improved with the addition of appropriate loss factors for sedimentation and grazing, and with the incorporation of a larger span of years to increase sample size. The latter consideration is particularly important for the summer period and for the separation of temperature and light effects in the spring. This type of analysis could be used on a long-term basis to detect shifts in controlling parameters and/or important associations, by looking for consistent changes in a series of analyses involving sequentially overlapping four-year blocks of data.

SAMPLING

The comparison of integrated and discrete depth estimates of epilimnetic concentrations of PON, POC, and CHLAU indicates that the discrete depth sample, even a DWA of two to three discrete depth samples, cannot always be depended upon to accurately represent epilimnetic conditions. Stratification of phytoplankton and zooplankton within the epilimnion is a well-known

phenomenon and can be more pronounced in some years than others. When living organisms stratify, nutrients and other chemicals which they use and produce may also become stratified. Therefore, for all parameters, epilimnetic estimates based on integrated samples should provide more accurate data for comparisons between years and within seasons than estimates derived from only two or three discrete depth samples. Integrated samples are also faster to collect and cheaper to analyze. Therefore, in terms of both accuracy and cost, they are more appropriate for long-term monitoring than discrete depth samples.

The accuracy of seasonal estimates is very dependent on sampling frequency, especially with biological variables. For POC, PON, and chlorophyll, biweekly sampling provided estimates within ±13 to ±19 percent of the weekly value. Horn (1984) examined the effect of sampling frequency on another biological variable, total algal biomass, in a meso-eutrophic lake in Denmark. She found moderate increases in variability with decreases in sampling intensity. Her ranges for weekly, biweekly, and four-weekly sampling were ±4, ±10, and ±16 percent of the twice-weekly value respectively. This variability is lower than that found in the present study for biological parameters. The difference may be due to a combination of technical (missing sample dates in the present study) and real (water-body characteristics) sources of variability. Nonetheless, both studies indicate that frequent sampling, preferably weekly, is necessary to estimate seasonal means and portray temporal patterns of biological variables. Nutrients (TKJN,NO3NO2, TP, TFP, SRS) and temperature showed less temporal variability than the biological parameters. With biweekly sampling, their estimate ranged from

±6 to ±10 percent. Therefore, the seasonal means of these variables could be based on less frequent sampling. Similarly the physical parameters (pH, $DISSO_2$, ALKA, CL) require even less frequent sampling due to the lack of variability in their temporal patterns. However, if the chemical, physical and biological variables are to be interrelated, the sampling frequency of the most variable parameters should be adopted for all measures.

SECTION TWO: PHYTOPLANKTON

RESULTS

PATTERNS IN ALGAL BIOMASS

Seasonal fluctuations in total and algal class biomasses were distinct in the mid-lake and nearshore regions (Figs. 6a, 6b). In the mid-lake region the patterns of peaks and troughs were similar between years (Fig. 7). Sequentially, the following events were observed: during the spring isothermal period, small to medium peaks occurred between Julian days 83 to 96 (Ai) and 112 to 118 (Aii), and a period of high biomass with peaks between days 154 to 168 (Bi) and 181 to 203 (Bii); following stratification, a trough in algal biomass developed, followed by a second period of high biomass with peaks between days 217 to 242 (Ci) and 266 to 278 (Cii); and a smaller peak occurred between days 307 to 315 (D) with the marked deepening of the epilimnion or return to isothermal conditions in the late fall. At Station 41 there was an additional peak between days 131 to 148 (E). The spring biomass peaks reached 1.08 to 1.51 $g.m^{-3}$ at station 12, and 1.10 to 1.17 $g.m^{-3}$ at station 41. The maximum summer biomasses ranged from 1.57 to 1.84 $g.m^{-3}$. In 1981, the autumn maxima ranged from 1.03 to 1.07 $g.m^{-3}$ while in 1982 they ranged between 0.39 and 0.59 $g.m^{-3}$. When each of these peaks was examined to determine which algal groups increased markedly at these times, that is, an increase in biomass >0.1 $g.m^{-3}$, it was found that the Bacillariophyceae and later Dinophyceae contributed most to the spring peaks (A, E). The Dinophyceae and Cryptophyceae were primarily responsible for the pre-trough

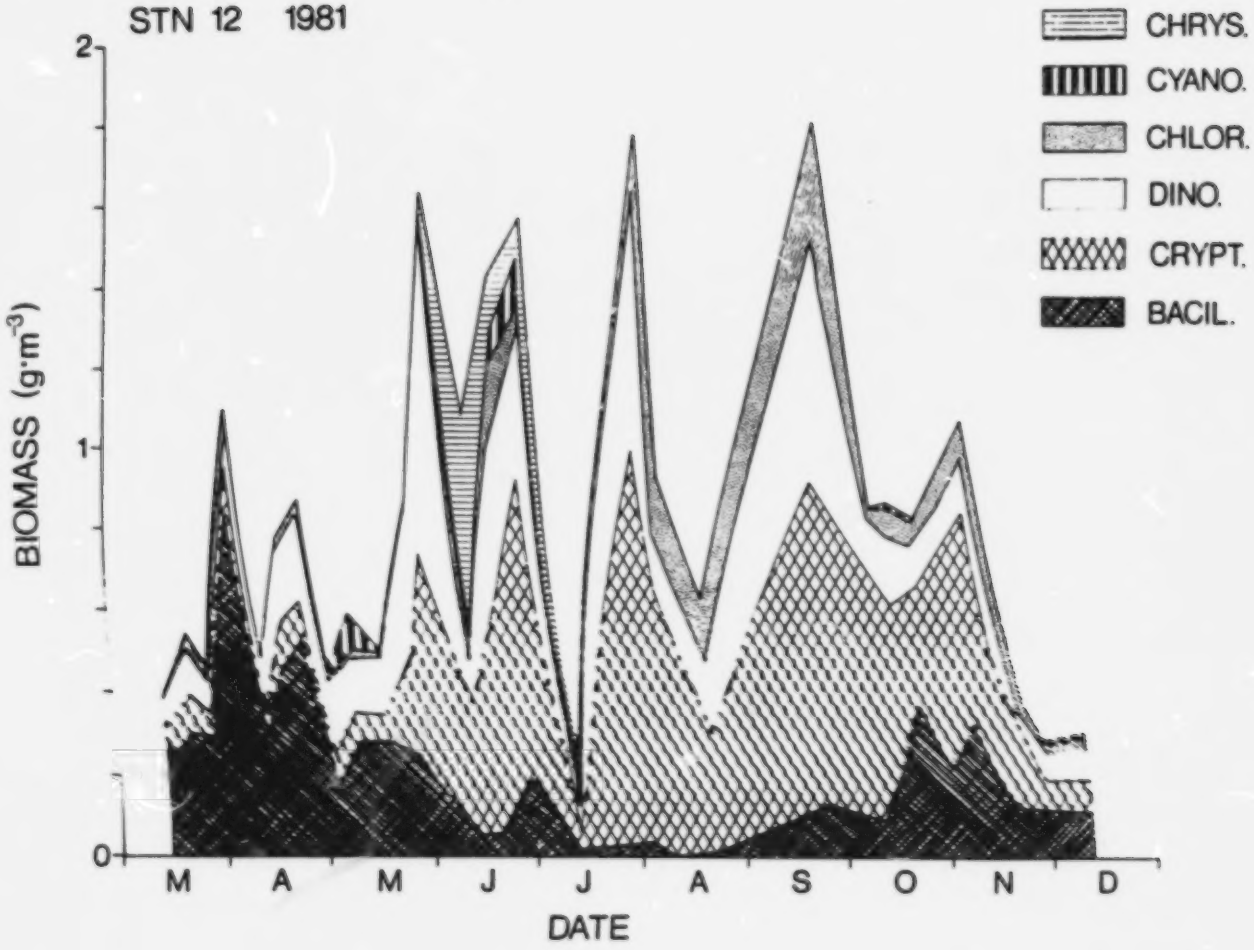


Figure 6a. Seasonal trends in total epilimnetic algal biomass for 1981, broken down by algal class.

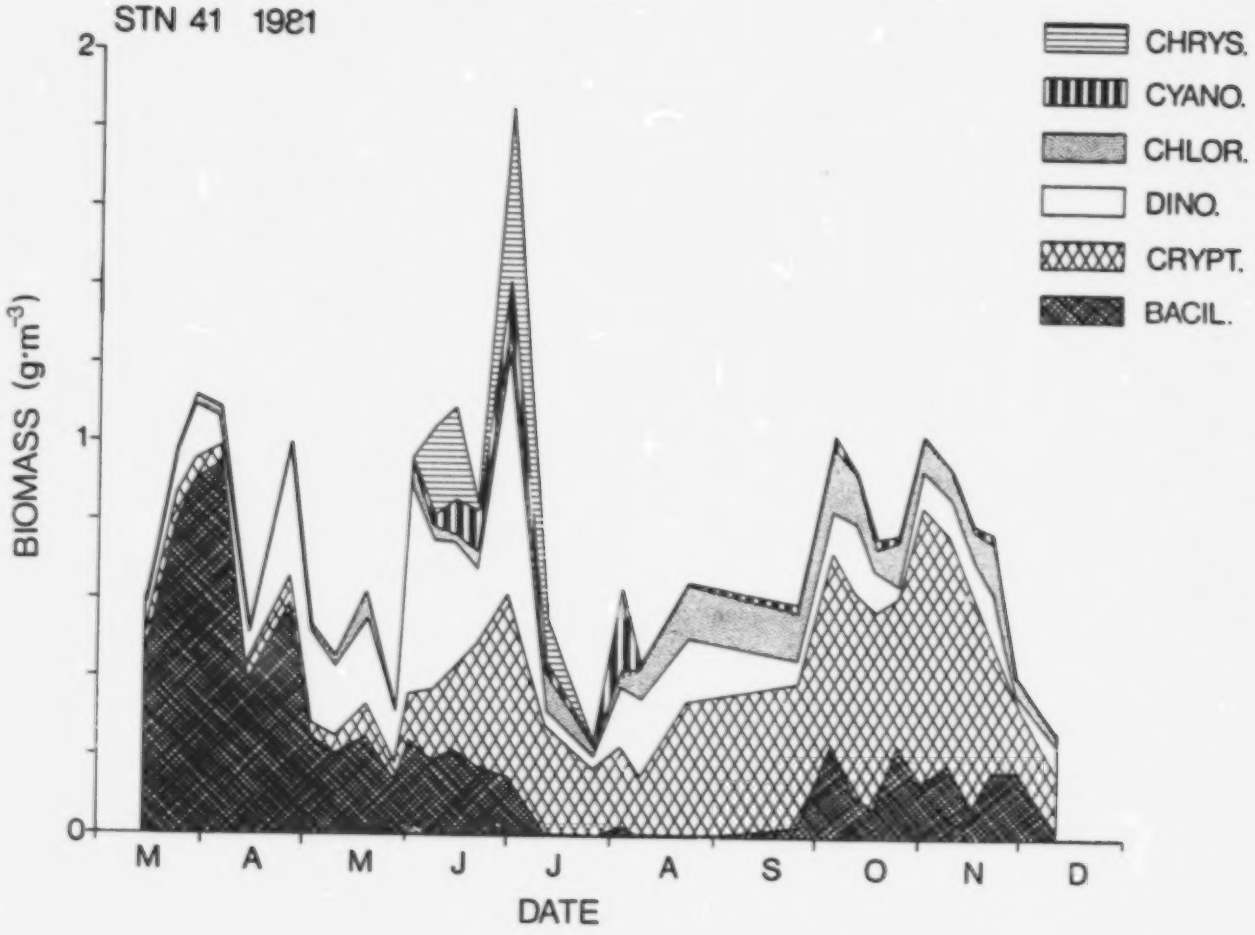
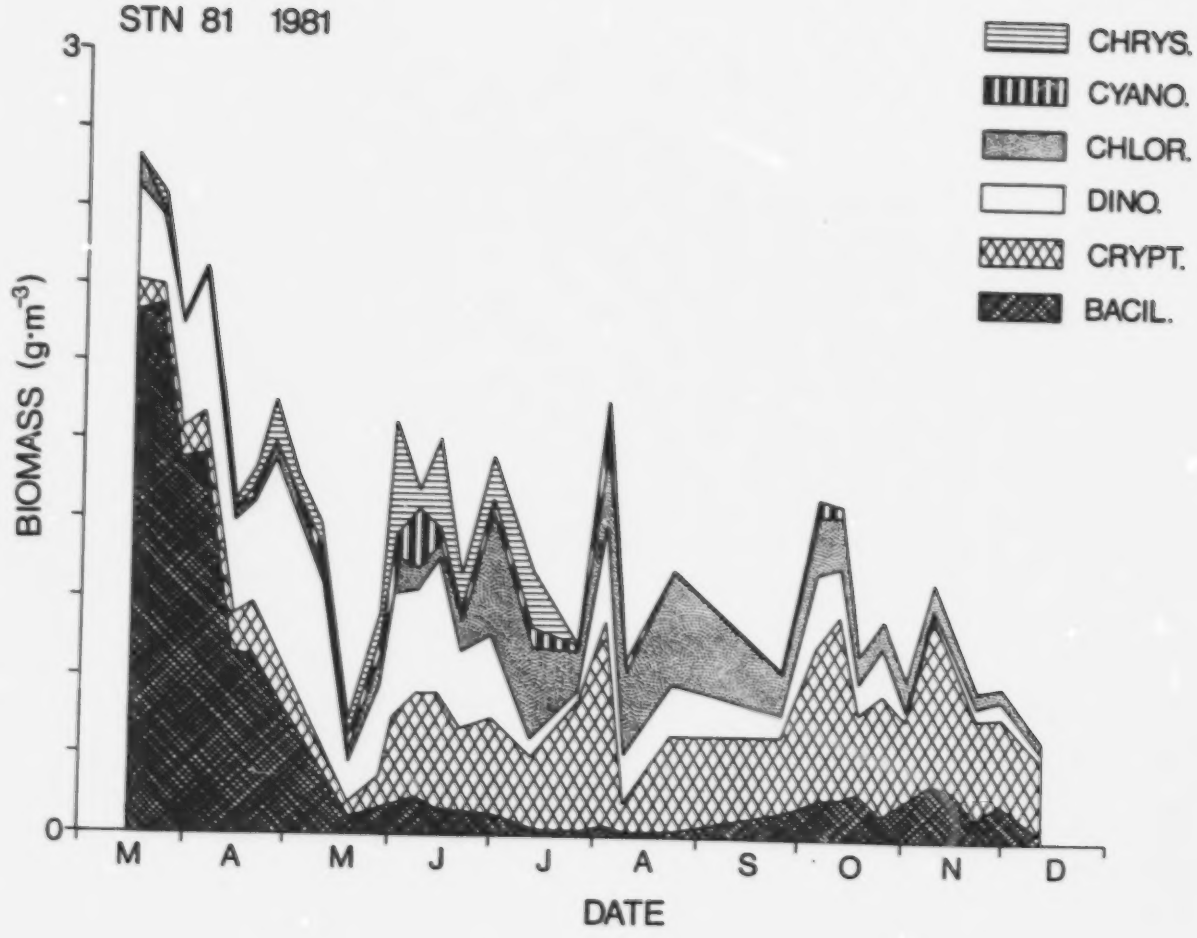


Figure 6a. Continued



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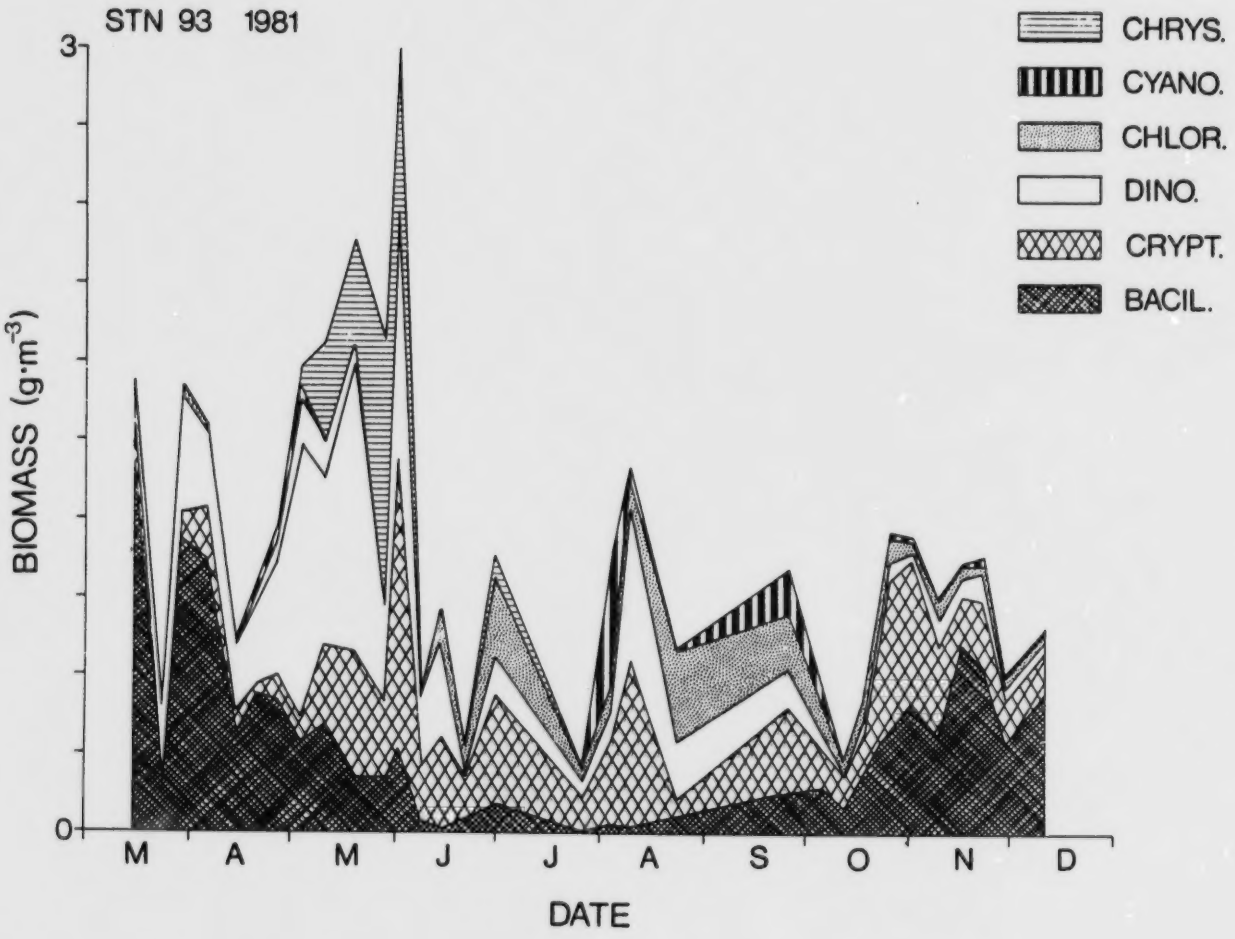

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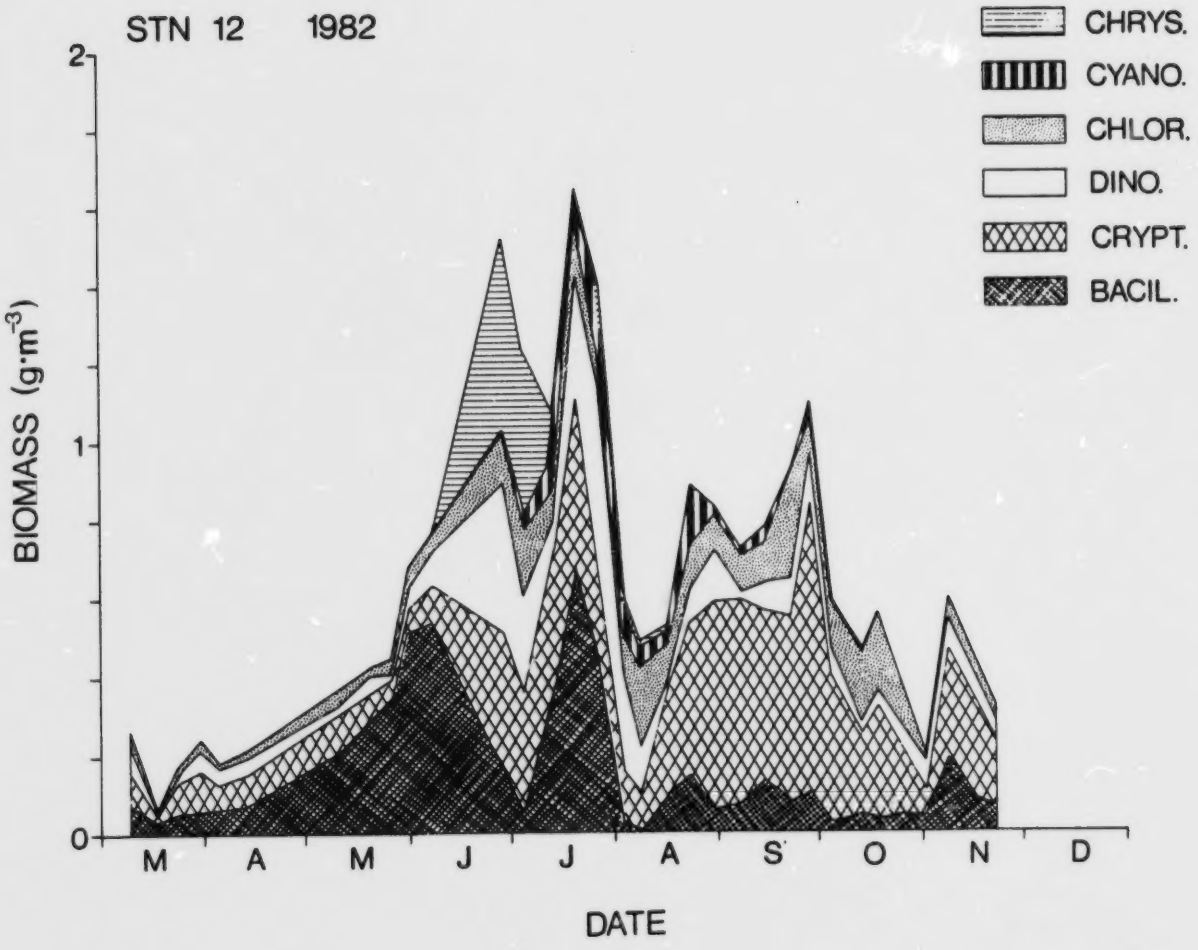
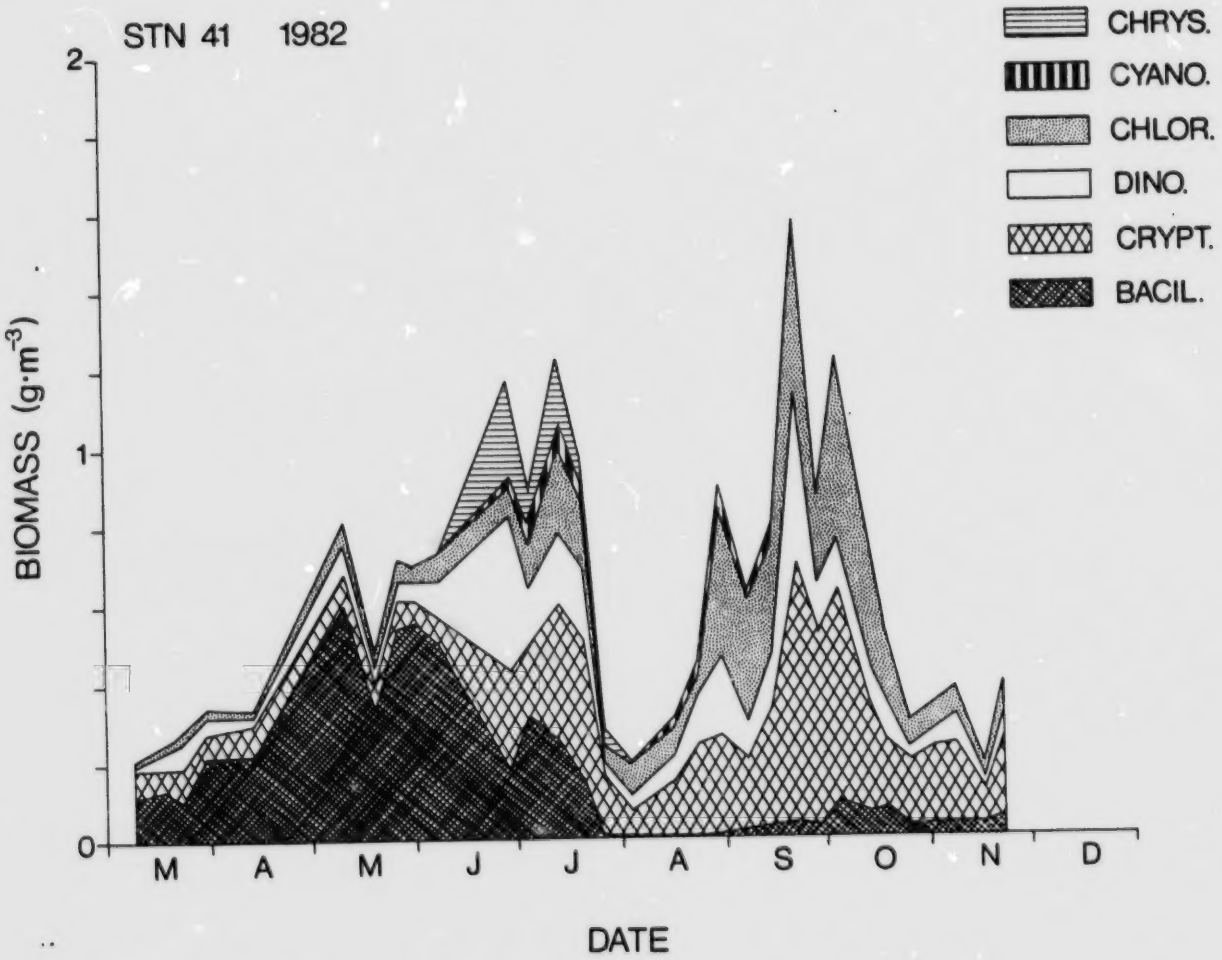


Figure 6b. Seasonal trends in total epilimnetic algal biomass for 1982, broken down by algal class.



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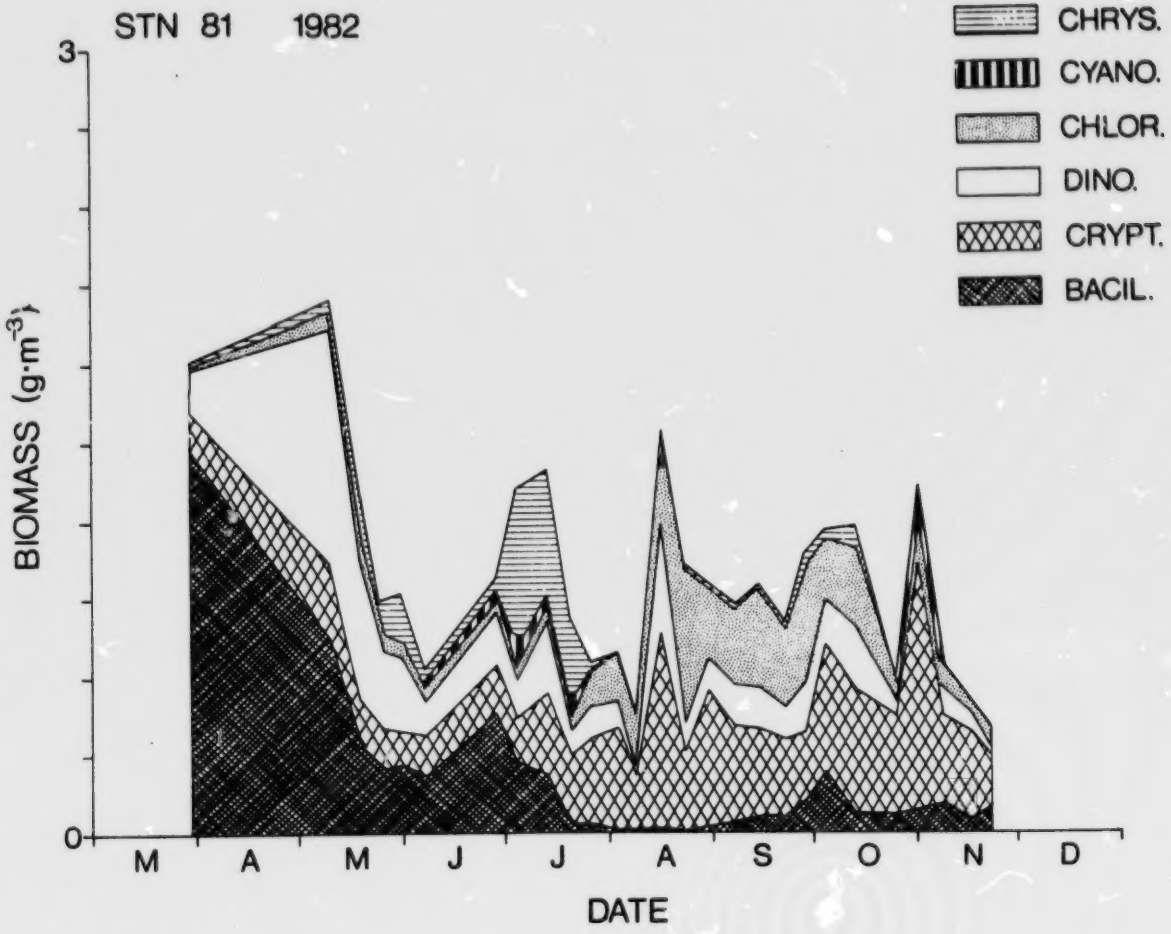

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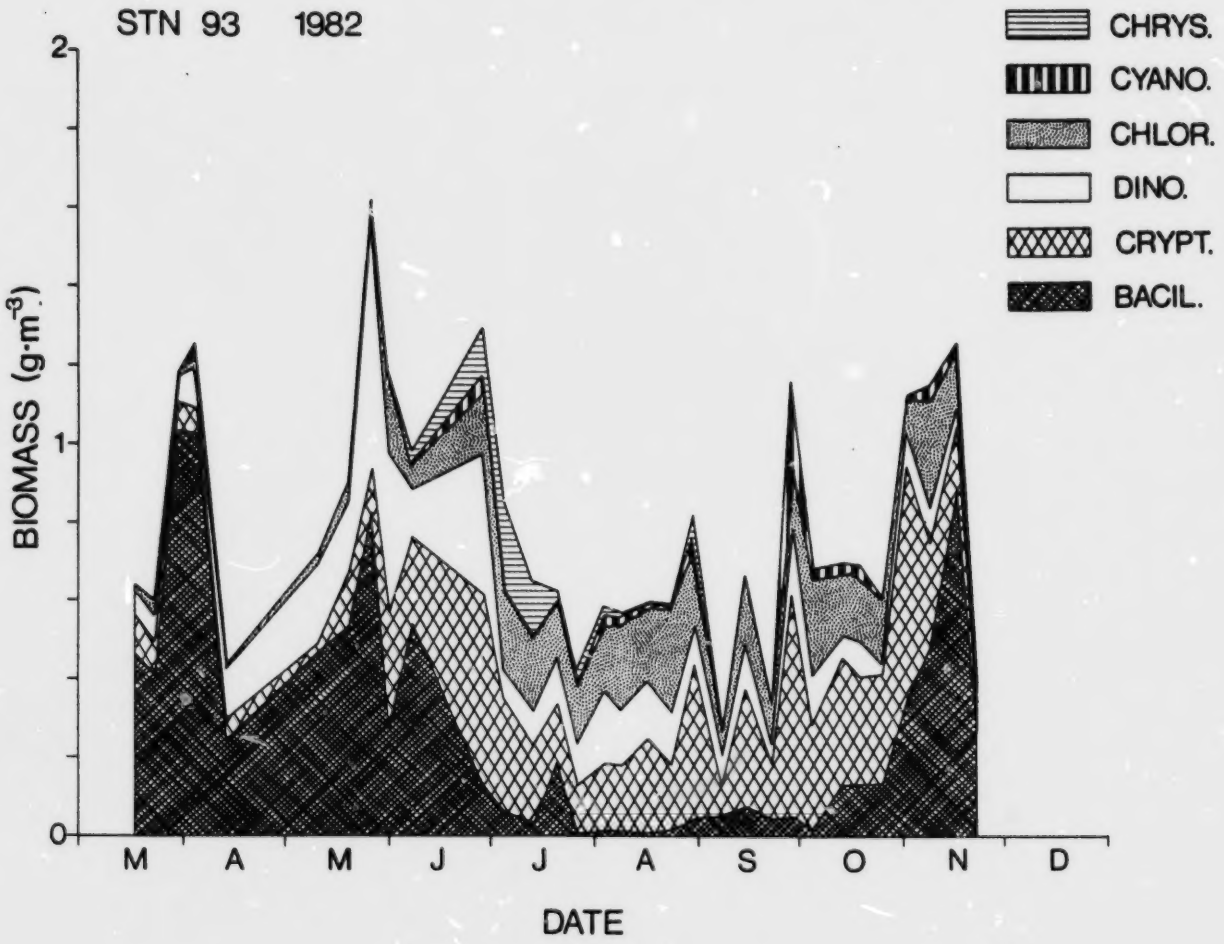

Figure 6b. Continued

Figure 7. A diagramatic representation of the temporal pattern of peaks and troughs in total algal biomass in the mid-lake region.

Explanation:

Bacillariophyceae	Bacil.	1) *Melosira binderana*
		2) *Stephanodiscus astrea* var. *minutula*
		3) *Synedra ulna*
		4) *Melosira islandica*
Dinophyceae	Dino.	5) *Gymnodinium helveticum*
		6) *Gymnodinium uberrimum*
		7) *Glenodinium* spp.
		8) *Peridinium aciculiferum*
		9) *Ceratium hirudinella*
Chrysophyceae	Chrys.	10) *Dinobryon sertularia*
Cryptophyceae	Crypt.	11) *Cryptomonas erosa*
		12) *Rhodomonas minuta*
Cyanophyceae	Cyano.	13) *Anabaena* sp.
Chlorophyceae	chlor.	14) *Sphaerocystis schroeteri*

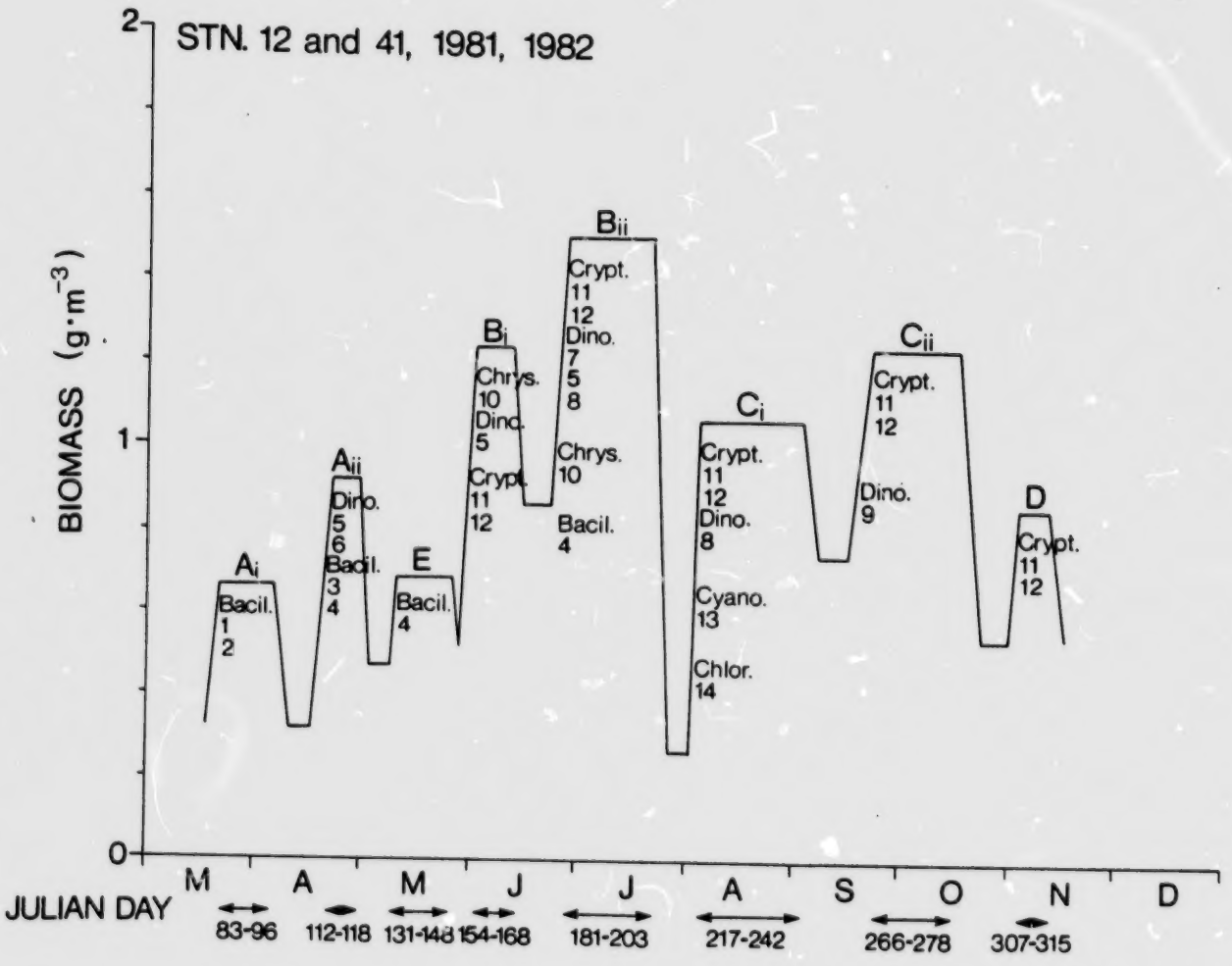

Figure 7. A diagramatic representation of the temporal pattern of peaks and troughs in total algal biomass in the mid-lake region. The dominant algal class(es) and species are given in the explanation on the previous page.

summer peaks (Bi, Bii):· the Chrysophyceae also contributed considerably to the first of these peaks (Bi). However, after the mid-summer trough in biomass the algal class structure of the phytoplankton peaks was more variable. The Cryptophyceae were important in the (Cii) peak and generally in the (Ci) peak, while the Dinophyceae contributed to the (Ci) peak at station 41. The late autumn peak (D) was composed of Cryptophyceae and Bacillariophyceae. The seasonal pattern in total biomass was principally the result of fluctuations in the Bacillariophyceae, Cryptophyceae and Dinophyceae.

The seasonal patterns in total biomass at the nearshore stations differed from that at the mid-lake sites. The inshore patterns were very variable although the seasonalities of the algal classes were similar. The periods of highest biomass occurred in the spring. At station 81, the maximum occurred between mid-March and mid-April, and was composed principally of Bacillariophyceae, while at station 93, the biomass peak continued from the end of April to the end of May (1981) or end of June (1982) and consisted of Bacillariophyceae and Dinophyceae. Thereafter, total biomass was lower with incomplete correspondence of peaks between seasons or stations. Chrysophyceae were the principle contributors to the late spring (days 147 to 154) and early summer (days 167 to 196) peaks observed at station 81 and also contributed significantly, though not usually more than other algal groups, to the same peaks at station 93. The Cryptophyceae more than any other group formed the backbone of the summer and autumn biomass peaks and were the major source of the commonality which did exist between years and stations. The Dinophyceae contributed significantly to the summer and autumn biomass peaks in 1981, but in 1982 were not important after mid-August. The Chlorophyceae were

sporadically important throughout this period. A November peak composed of Cryptophyceae and Bacillariophyceae was present at both stations in both years.

The spring biomass peaks at station 81 were the highest of all four stations observed, being 2.04 and 2.59 $g.m^{-3}$, while at station 93 they were 1.62 and 1.72 $g.m^{-3}$. In the summer they usually reached maxima of 1.29 to 1.66 $g.m^{-3}$. In 1981 at station 93, the peak reached the unusually high level of 2.99 $g.m^{-3}$. The maximum autumn peaks were lower, varying from 0.98 to 1.33 $g.m^{-3}$.

In examining biomass trends, the data for each cruise were first separated into five time periods, defined previously for the chemical data. A three way analysis of variance was applied, examining the effect of years, station location, and season (Table 9). As expected, all groups varied seasonally. In addition, the Cryptophyceae, Bacillariophyceae, Dinophyceae and total algal biomass differed significantly between years and among stations ($p<0.05$). The biomasses of all three algal classes were greater in 1981 than in 1982 and at nearshore as compared with mid-lake stations (Fig. 8). Similarly, seasonally weighted mean algal biomass was lower in 1982 than in 1981 and at mid-lake as compared to nearshore stations (Table 10). Between the two years, the mid-lake seasonally weighted mean biomasses decreased from 0.92 to 0.76 $g.m^{-3}$ in 1981 to 0.64 to 0.63 $g.m^{-3}$ in 1982, and the biomass at the nearshore station 93, decreased from 1.15 $g.m^{-3}$ to 0.80 $g.m^{-3}$. The biomass at station 81 remained relatively constant at 1.10 to 1.15 $g.m^{-3}$.

TABLE 9: Analysis of variance results assessing the effect of year, station location and season on the abundance of the various algal classes. All significant values ($p < 0.05$) are underlined.

ALGAL CLASS	Probability of "F" Due To					
	Year	Station	Season	Year-Station	Year-Season	Season-Station
Chlorophyceae	0.767	0.374	<u>0.002</u>	0.169	0.926	0.692
Euglenophyceae	0.436	0.314	0.143	0.176	0.938	0.921
Cyanophyceae	0.355	0.991	<u>0.001</u>	0.074	0.079	0.468
Cryptophyceae	<u>0.002</u>	<u>0.037</u>	<u>0.001</u>	0.560	0.280	<u>0.013</u>
Dinophyceae	<u>0.001</u>	<u>0.018</u>	<u>0.001</u>	0.366	<u>0.008</u>	<u>0.001</u>
Chrysophyceae	0.808	0.775	<u>0.001</u>	0.202	0.993	0.999
Bacillariophyceae	<u>0.006</u>	<u>0.001</u>	<u>0.001</u>	0.913	<u>0.010</u>	<u>0.001</u>
TOTAL	<u>0.001</u>	<u>0.001</u>	<u>0.001</u>	0.126	0.867	<u>0.001</u>

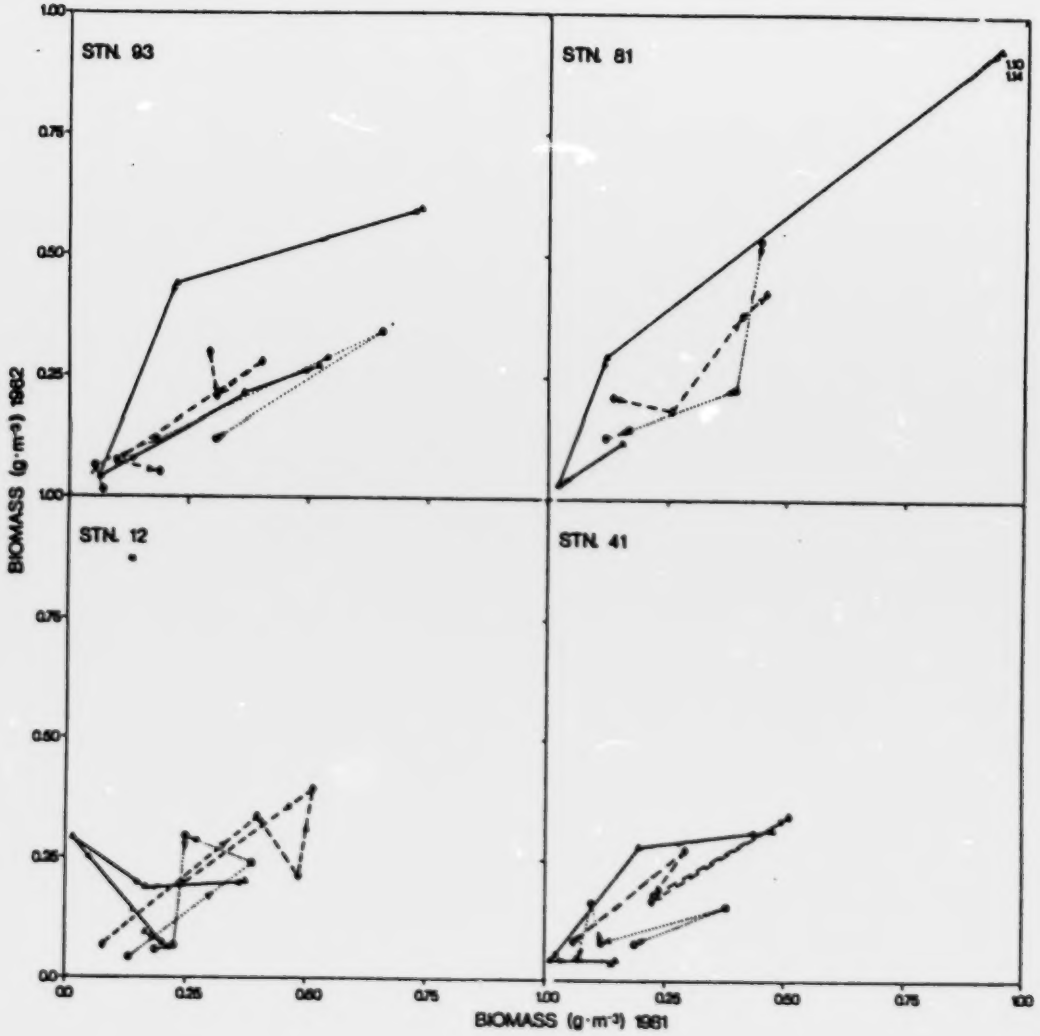

Figure 8. A comparison amongst the four stations and between the two years of the average thermal period biomasses of the Bacillariophyceae (▲), Cryptophyceae (■), and Dinophyceae (●).

TABLE 10: Seasonally weighted mean algal biomass ($g.m^{-3}$).

Station	1981	1982	% Change (82/81)
12	0.92	0.64	-43.8
41	0.76	0.63	-20.6
81	1.10	1.15	+4.4
93	1.15	0.80	-43.8

The algal class percentage composition, however, was consistent among stations and between years. This was determined by chi square tests applied to the arcsine transformed percentage composition data. The most important groups were the Cryptophyceae, Bacillariophyceae and Dinophyceae, which together contributed over 80 percent of the total seasonal biomass (Fig. 9). This is in contrast to their biomasses which differed between years and amongst stations (see above).

SPECIES COMPOSITION

One hundred and fifty algal species, varieties or genera were identified for Lake Ontario (Johannsson et al., 1985), but not all of these are important to the phytoplankton community biomass. The important algae were defined as those contributing 5 percent or more to the biomass of any one sample over the two year period (Table 11). The percentage contribution of these species to the sample biomasses were examined at each station. The year was divided into the five seasonal-thermal periods described previously and lists were constructed for each period of the species contributing five to ten percent or greater than ten percent to the biomass of at least one sample. Since the lists were more similar for stations 12 and 41 and for stations 93 and 81, the data were grouped as nearshore and mid-lake. Figure 10 shows the seasonal pattern of importance and the relative degree of importance of each species to the sample biomass.

The information for the two years for the two stations were collated, thereby providing four observations for each species for each

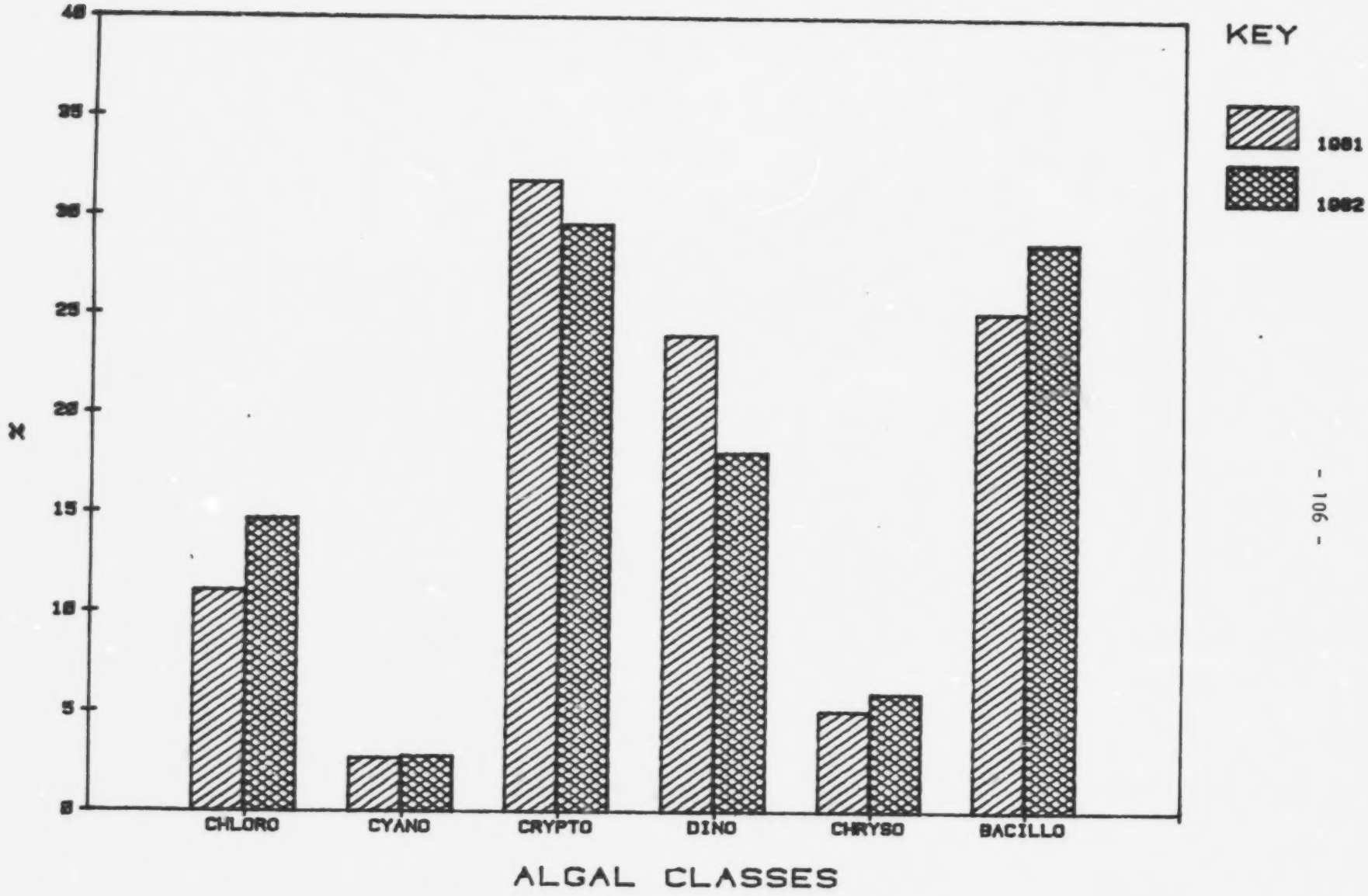

Figure 9. Percent contribution of each algal class to total seasonal biomass in 1981 and 1982.

TABLE 11: Historical survey of key algal species in Lake Ontario contributing >5 percent to sample biomass at any one time. Three asterisks denote dominant species as mentioned by the authors, one asterisk denotes presence >5 percent, and a dash indicates absence or presence <5 percent.

	1966-68[2]	1970	1972	1981-82[1]
BACILLARIOPHYCEAE				
Cyclotella spp.	–	–	–	***
Tabellaria flocculosa	–	–	–	***
Synedra ulna	–	*	–	***
Stephanodiscus niagarae	*	***	–	***
Tabellaria fenestrata	*	*	***	***
Melosira islandica	*	–	***	***
Stephanodiscus astrea var. minutula	*	–	***	***
Melosira binderana	*	***	***	***
Stephanodiscus hantzschii	*	***	***	***
Diatoma tenue var. elongatum	*	–	***	***
Nitzschia linearis	–	–	***	***
Stephanodiscus subtilis	–	–	***	–
Stephanodiscus alpinus	–	–	***	–
Nitzschia acicularis	*	–	***	–
Synedra acus	–	–	***	*
Nitzschia bacata	–	–	***	–
Nitzschia dissipata	–	–	***	–
Surirella angusta	–	–	***	–
Asterionella formosa	*	***	***	*
Stephanodiscus tenuis	*	***	***	–
Asterionella gracillima	–	***	–	–
Surirella ovalis	–	–	***	–
Melosira varians	–	***	–	–
Stephanodiscus hantzschii var. pusilla	–	***	–	–
Nitzschia sigmoidea	*	–	–	–
Nitzschia holsatica	*	–	–	–
Fragilaria crotonensis	*	*	–	*
Fragilaria capucina	*	–	–	–
Navicula sp.	–	*	–	–
Nitzschia palea	–	*	–	–
Synedra utermohlii	–	*	–	–
Tabellaria spp.	–	*	–	–
Stephanodiscus astrea	*	*	–	–
Cocconeis pediculus	*	–	–	–
CRYPTOPHYCEAE				
Cryptomonas erosa	*	***	***	***
Rhodomonas minuta	–	***	***	***
Katablepharis ovalis	–	***	*	–
Cryptomonas curvata	–	*	*	–
Cryptaulax rhomboidea	–	*	–	–
DINOPHYCEAE				
Gymnodinium helveticum	–	***	***	***
Peridinium aciculiferum	–	–	***	***
Glenodinium spp.	–	*	***	***
Ceratium hirudinella	*	*	***	***
Gymnodinium uberrimum	–	–	***	***
Peridinium cinctum	–	–	–	***
Glenodinium pulviscules	–	*	–	–
CHRYSOPHYCEAE				
Gyromitus cordiformis	–	*	–	–
Dinobryon sertularia	–	–	–	***(***)
Dinobryon sociale	*	*	–	***(-)
Dinobryon divergens	–	–	–	***(-)
Chrysochromulina parva	–	***	***	?
Chromulina spp.	–	*	–	–
Ochromonas spp.	–	*	–	–

	1966-68	1970	1972	1981-
CHRYSOPHYCEAE				
Dinobryon spp.	*	–	–	–
Trachelomonas spp.	*	–	–	–
CYANOPHYCEAE				
Anabaena spp.	*	–	–	**
Oscillatoria minima	–	–	–	**
Oscillatoria limnetica	–	***	***	**
Oscillatoria bornelli	–	–	***	–
Chroococcus dispersus var. minor	–	***	*	–
Aphanizomenon flos-aquae	–	*	–	–
Aphanocapsa spp.	–	*	–	–
Gomphosphaeria aponina	–	*	–	–
Oscillatoria planctonica	*	–	–	–
Gomphosphaeria spp.	*	–	–	–
CHLOROPHYCEAE				
Mougeotia spp.	*	*	–	**
Oocystis spp.	–	*	–	**
Sphaerocystis schroeteri	–	–	*	**
Staurastrum paradoxum var. parvum	–	–	–	**
Pediastrum simplex var. doudenarium	–	–	–	**
Pediastrum duplex var. clathratum	–	–	–	**
Staurastrum paradoxum	–	*	***	**
Chlamydomonas spp.	–	–	***	75
Ankistrodesmus setigerus	–	–	***	–
Gloeocystis planctonica	–	–	***	–
Lagerheimia ciliata	–	*	***	–
Phacotus lenticularis	–	*	***	–
Pediastrum simplex	–	–	***	–
Scenedesmus quadricauda var. quadrispina	–	–	***	–
Ulothrix subconstricta	–	–	***	–
Scenedesmus bijuga	–	***	***	*
Ankistrodesmus falcatus	*	***	***	–
Ankistrodesmus falcatus var. spirilliformis	–	***	–	–
Chlamydomonas globosa	–	***	–	–
Chlorella spp.	–	***	–	–
Coelastrum microporum	–	***	–	*
Oedogonium spp.	–	***	–	–
Pedinomonas minutissma	–	***	–	–
Ankistrodesmus falcatus var. mirabilis	–	*	–	–
Asterococcus spp.	–	*	–	–
Carteria cordiformis	–	*	–	–
Closterium limneticum	–	*	–	–
Coelastrum proboscideum	–	*	–	–
Cosmarium spp.	–	*	–	*
Gloeocystis ampla	–	*	–	–
Oocystis borgei	*	*	–	–
Scenedesmus quadricauda	–	*	–	–
Staurastrum spp.	*	*	–	–
Tetraedron spp.	–	*	–	–
Ulothrix subtilissmia	–	*	–	–
Dictosphaerium ehrenbergianum	*	–	–	–
Micractinium pusillum	*	–	–	–

1. Data were collated from the following papers:
   1966-68 - Michalski (1968), Nalewajko (1966, 1967), Sreenivasa and Nalewajko (1975)
   1970 - Munawar and Munawar (1981), Munawar and Nauwerck (1971)
   1972 - Munawar *et al* .(1974), Stoermer and Ladewski (1984)

2. Data from the late 1960's comprise those species reported as important by the authors, judged on a numerical basis.

3.
   a) *Scenedesmus bijuga* is probably *S . bicellularis* of Stoermer *et al* . (1975)
   b) *Synedra acus* includes both *S . acus* (Munawar *et al* ., 1974) and *S . a* . var. *ostenfeldii* (Stoermer *et al* .,
1975)

4. The bracketed values are based on protoplast not lorica volumes.

5. In 1981 and 1982 *Chrysochromulina parva* was also included in *Chlamydomonas* spp.

A) Stations 12,41

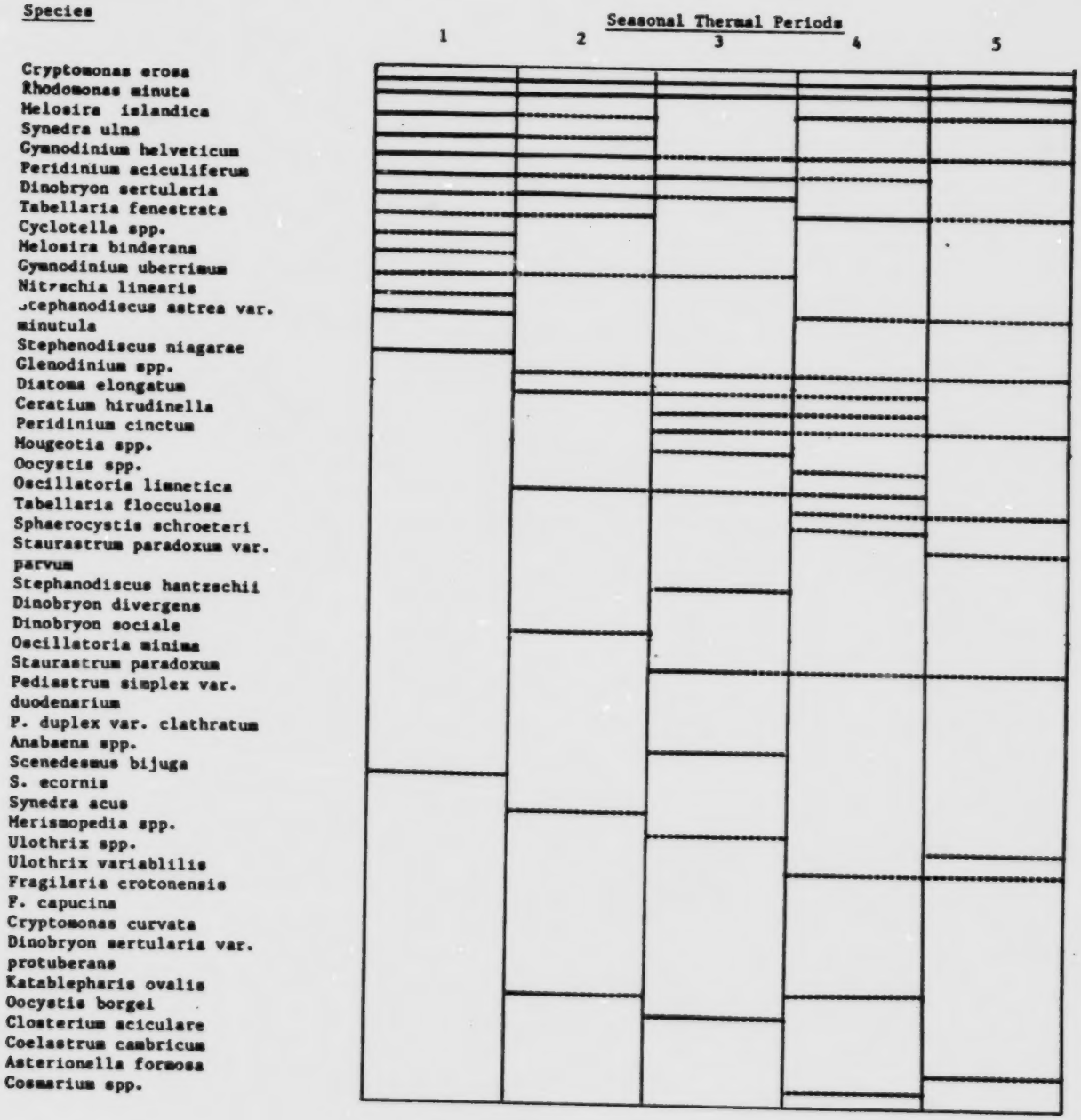

FIGURE 10. Seasonal patterns of species abundance for species contributing more than 5% of sample biomass in 1981 or 1982. A solid line denotes repeated contributions greater than 10% (both stations, both years); a dashed line, sporadic contributions greater than 10% and a dotted line, contributions greater than 5%. Thermal period temperature ranges are as follows: 1)0.0-5.9°C, 2)6.0-16.9°C, 3)17.0+°C, 4)16.9-8.0°C and 5)7.9-0.0°C. See text for description of seasonal periods.

B) Stations 81,93

Species

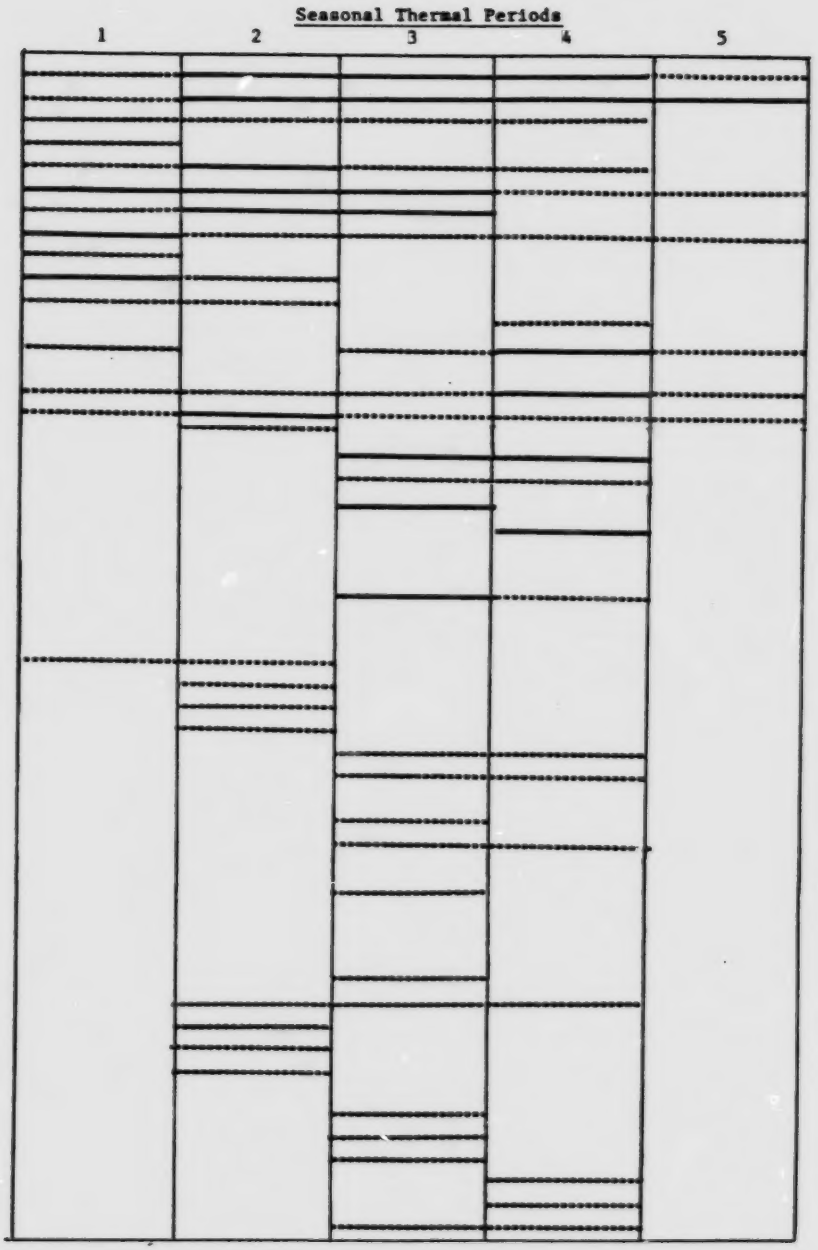

Figure 10. Continued

seasonal-thermal period. If a species contributed more than ten percent in three or four of the four possible observations it was considered to be a "PRINCIPAL" species in that seasonal-thermal community and in Figure 10 its presence is marked with a solid line. If it contributed more than ten percent only once or twice in the period, it was considered to be a "MAJOR" species and is denoted by a dashed line. If a species contributed between 5 to 10 percent at least once it was considered "IMPORTANT" and is represented by a dotted line. Inspection of the figures reveals that the same species are generally important at all stations, but their relative importance and timing differ between the nearshore and mid-lake. At all stations, Cryptomonas erosa, Rhodomonas minuta, Gymnodinium helveticum, Peridinium aciculiferum, Dinobryon sertularia and Tabellaria fenestrata were "PRINCIPAL" species. In addition, Melosira islandica and Synedra ulna were "PRINCIPAL" species at the mid-lake stations, and Melosira binderana, Stephanodiscus astrea var. minutula, S. niagarae, Glenodinium spp., Ceratium hirudinella, Mougeotia spp., Oocystis spp. and Sphaerocystis schroeteri were "PRINCIPAL" species at the nearshore stations. The "MAJOR" species common to both sets of stations were Gymnodinium uberrimum, Diatoma tenue var. elongatum, Peridinium cinctum and Anabaena spp. The "MAJOR" species characteristic of the mid-lake stations included all of the "PRINCIPAL" species listed above as specific to the nearshore stations, plus Cyclotella spp., Nitzschia linearis, Oscillatoria limnetica, Tabellaria flocculosa, and Staurastrum paradoxum var. parvum. Similarly, the "MAJOR" species of the nearshore stations included those "PRINCIPAL" species characteristic only of the mid-lake stations plus Stephanodiscus hantzschii, Dinobryon divergens, D. sociale, Oscillatoria

minima, Staurastrum paradoxum, Pediastrum simplex var. duodenarium, P. duplex var. clathratum, and Anabaena spp. Of the "IMPORTANT" species, not all occurred at both the mid-lake and nearshore stations. However, Fragilaria crotonensis, Katablepharis ovalis, Oocystis borgei, Asterionella formosa and Cosmarium spp. were common to both.

If the Chrysophyceaen species of Dinobryon were evaluated on the basis of protoplast instead of lorica volume, none of them would be "PRINCIPAL" species, and only D. sertularia would be a "MAJOR" species in the mid-lake and an "IMPORTANT" species nearshore.

The major contributors to the first thermal period (0° to 5.9°C) were the Bacillariophyceae, Melosira islandica, M. binderana, Synedra ulna, Tabellaria fenestrata, Stephanodiscus niagarae, S. astrea var. minutula, Nitzschia linearis, Cyclotella spp. and S. hantzschii; the Dinophyceae, Gymnodinium helveticum, G. uberrimum, Peridinium aciculiferum and Glenodinium spp., and the Chrysophyceaen, Dinobryon sertularia. Few Bacillariophyceae extended into the second thermal period; only M. islandica at the mid-lake stations, and T. fenestrata, M. islandica and S. niagarae at the nearshore stations. The Dinophyceae and Chrysophyceae, however, extended through and were joined by D. divergens, D. sociale, Oscillatoria minima and Diatoma tenue var. elongatum. During the height of the summer, thermal period three (17°C+), Bacillariophyceae were almost absent from the samples. Melosira islandica could occur nearshore along with lesser amounts (5 to 10 percent) of S. niagarae, S. astrea var minutula and T. fenestrata. Only D. tenue var. elongatum occurred in the mid-lake areas at these lower levels. Again the Dinophyceae extended through the summer, and many other species from different

groups became important at this time: Ceratium hirudinella, P. cinctum, Anabaena spp., Mougeotia spp., Sphaerocystis schroeteri, Staurastrum paradoxum, Pediastrum simplex var. duodenarium, and P. duplex var. clathratum. As temperatures fell in the autumn, entering thermal period four (16.9° to 8.0°C) some Bacillariophyceae regained their importance: T. fenestrata, T. flocculosa, S. astrea var. minutula and S. niagarae. Gymnodinium helveticum, P. aciculiferum, and Glenodinium spp., continued to be important and many of the summer species carried through: C. hirudinella, Oocystis spp., O. limnetica, S. schroeteri and Anabaena spp. Most species were gone by the last thermal period (7.9° to 0.0°C). This period was not sampled extensively because it began between the end of October and beginning of December when the research vessels were docked for the winter. The most important species were T. fenestrata, S. niagarae, S. paradoxum var. parvum, G. helveticum, P. aciculiferum and Glenodinium spp.

The main difference between the nearshore and mid-lake stations, other than the differences in the ranking of the species discussed above, was the more extended seasonal distributions at the nearshore stations, particularly of several Bacillariophyceae. Stephanodiscus astrea var. minutula, S. niagarae and Tabellaria fenestrata maintained 5 to 10 percent biomass levels in the summer nearshore, but not in the mid-lake.

In spite of the large diatom peaks in the spring, the most important species in terms of their seasonally weighted mean biomasses, were Cryptomonas erosa and Rhodomonas minuta. Cryptomonas erosa seasonally weighted mean biomass averaged from 0.0138 to 0.0222 $g.m^{-3}$, and that of R. minuta, from 0.0106 to 0.0140 $g.m^{-3}$. A controlled comparison of identification suggests that the C. erosa and R. minuta biomasses may be overestimated as Cryptomonas

rostrata, and C. pyrenoidifera were also identified as C. erosa, and Rhodomonas lens, Ochromonas sp., Cryptomonas tenuis and C. pyrenoidifera as R. minuta (Johannsson, unpublished data). However C. erosa and R. minuta are the dominant forms in Lake Ontario (Munawar et al., 1974), Melosira islandica, M. binderana or Stephanodiscus niagarae could be as abundant on occasions, but they usually fell in the second group of species with seasonally weighted averages between 0.0025 to 0.0095 $g.m^{-3}$. Gymnodinium helveticum, Peridinium aciculiferum, Glenodinium spp., Dinobryon sertularia, and Tabellaria fenestrata, were regular members of this second group, while Synedra ulna, Ceratium hirudinella, S. astrea var. minutula, Diatoma tenue var. elongatum, Oscillatoria limnetica, Oocystis spp., Sphaerocystis schroeteri, Gymnodinium uberrimum, and S. hantzschii were occasional members.

Algae identified as Chlamydomonas spp., unfortunately included Chrysochromulina parva, and these two species have not been included in the species results. Together, however, they constituted "a MAJOR species."

The seasonal patterns observed above do not necessarily reflect changes in the populations of the individual species. The seasonal population dynamics of the "PRINCIPAL" and "MAJOR" species are presented schematically in Figures 11 and 12 for the mid-lake and nearshore stations respectively, and in detail in Johannsson et al., (1985). The timing and overlap of periods of elevated species abundances differed slightly from year to year and station to station. Thus the periods of the year when population maxima can occur are portrayed as follows: solid lines represent periods when peaks were observed repeatedly between years and stations; and dashed lines, when peaks occurred occasionally. Besides this seasonal information, the figures also

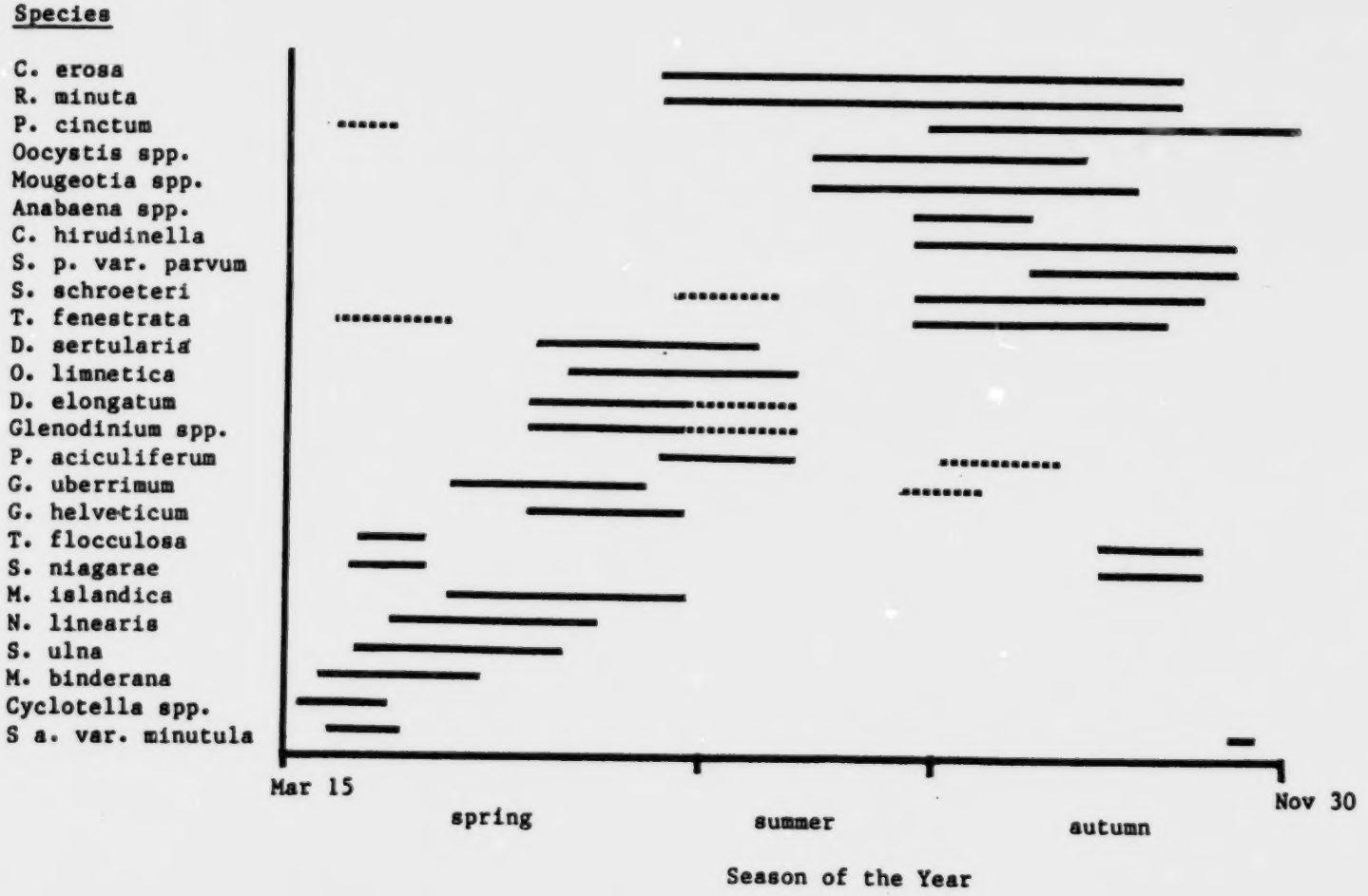

Figure 11. Stations 12 and 41. Schematic of phytoplankton population dynamics illustrating periods of potential population peaks. Solid lines indicate periods in which peaks regularly occurred; dashed lines, periods of sporadic occurrence.

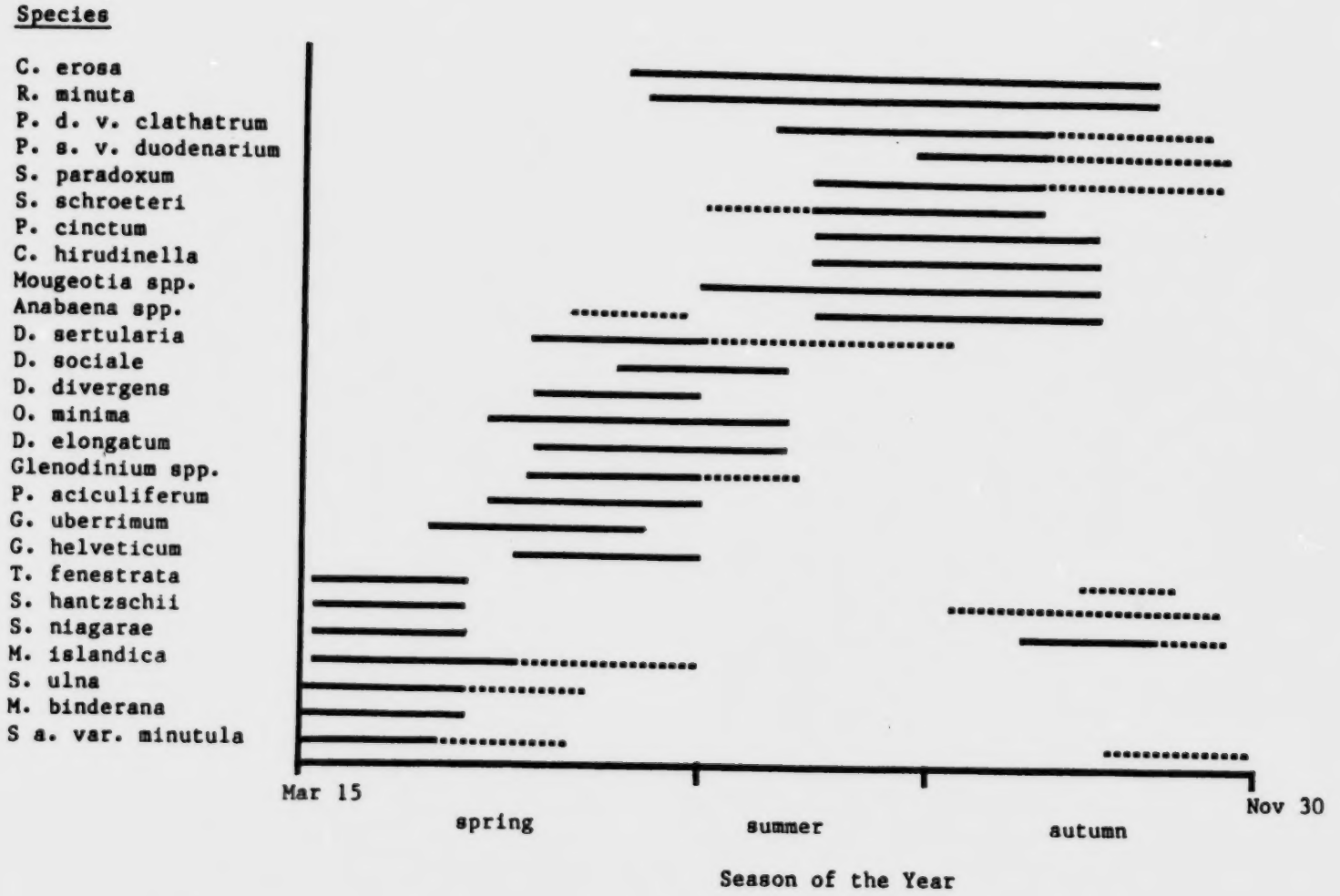

Figure 12. Stations 81 and 93. Schematic of phytoplankton population dynamics illustrating periods of potential population peaks. Solid lines indicate periods in which peaks regularly occurred; dashed lines, periods of sporadic occurrrence.

provide a measure of the co-occurrence or overlap between species. Only one seasonal pattern, collated from these figures, is described below. It includes all species which occurred at levels greater than ten percent at either the mid-lake or nearshore stations.

There were two distinct Bacillariophycean assemblages in the spring which separated or merged depending on the seasonal conditions. The early spring group consisted of Tabellaria fenestrata, Melosira binderana, Cyclotella spp., Stephanodiscus astrea var. minutula, S. niagarae and S. hantzschii. The mid-spring assemblage contained M. islandica, Synedra ulna and Nitzschia linearis. Irrespective of the seasonal patterns of the Bacillariophycean groups, a third group peaked during mid to late spring. It was composed of alga from many classes: Peridinium aciculiferum, Gymnodinium uberrimum, G. helveticum, Glenodinium spp., Diatoma tenue var. elongatum, Oscillatoria limnetica, Dinobryon sertularia, D. sociale, and D. divergens. All spring species blooms were finished or were finishing by early summer. There was a period of transition when few species were important and Cryptomonas erosa and Rhodomonas minuta, which bloom from late spring to early autumn, were the principal species present. Then Oocystis spp., Mougeotia spp., and Pediastrum duplex var. clathratum started to peak in mid-summer. They were joined during late summer and early autumn by T. fenestrata, Sphaerocystis schroeteri, Ceratium hirudinella, Anabaena spp. Peridinium cinctum, and Staurastrum paradoxum. These in turn overlapped with the still later starting P. simplex var. duodenarium and S. paradoxum var. parvum. During mid to late autumn most species were either decreasing or gone. The Bacillariophyceae, T. flocculosa, S. niagarae, S. hantzschii and S. astrea var. minutula frequently regained importance in the autumn, especially at the mid-lake stations.

SAMPLING FREQUENCY

Phytoplankton species can grow very rapidly, and the frequency of sampling must be high in order to follow changes in community structure. The adequacy of different sampling frequencies was assessed by calculating the Percent Dissimilarity between phytoplankton communities separated by one, two, three, four, five, and six-week intervals. All the 1981 and 1982 data were included in the analysis. The mean dissimilarities from all stations were averaged and compared with the variability in Percent Dissimilarity amongst 64 pairs of replicate samples taken throughout the study period. Percent Dissimilarity increased linearly with sampling frequency over the six-week period (Fig. 13).

Changes in phytoplankton community structure can be followed adequately with weekly sampling. The Percent Dissimilarity amongst samples collected at an interval of one week was very similar to the dissimilarity of replicate samples (Fig. 13).

DISCUSSION

Many changes have occurred in Lake Ontario within the past 15 years. The lake has been subjected to exponentially increasing salmonid stocking and a sharp decline in phosphorous loading since the early 1970s. Mid-lake spring phosphorous levels peaked in 1973 at 0.031 $g.m^{-3}$: by 1982 they had decreased to 0.013 $g.m^{-3}$ (Stevens and Neilson, in prep.). Summer levels have not shown as marked a change, decreasing from 0.017 $g.m^{-3}$ in 1969 to only 0.014 $g.m^{-3}$ in 1982. Algal growth in many natural systems is limited by phosphorous concentrations; indeed, in areas where nutrient addition tests have been performed in the Great Lakes - Lakes Superior, Michigan, and Huron -

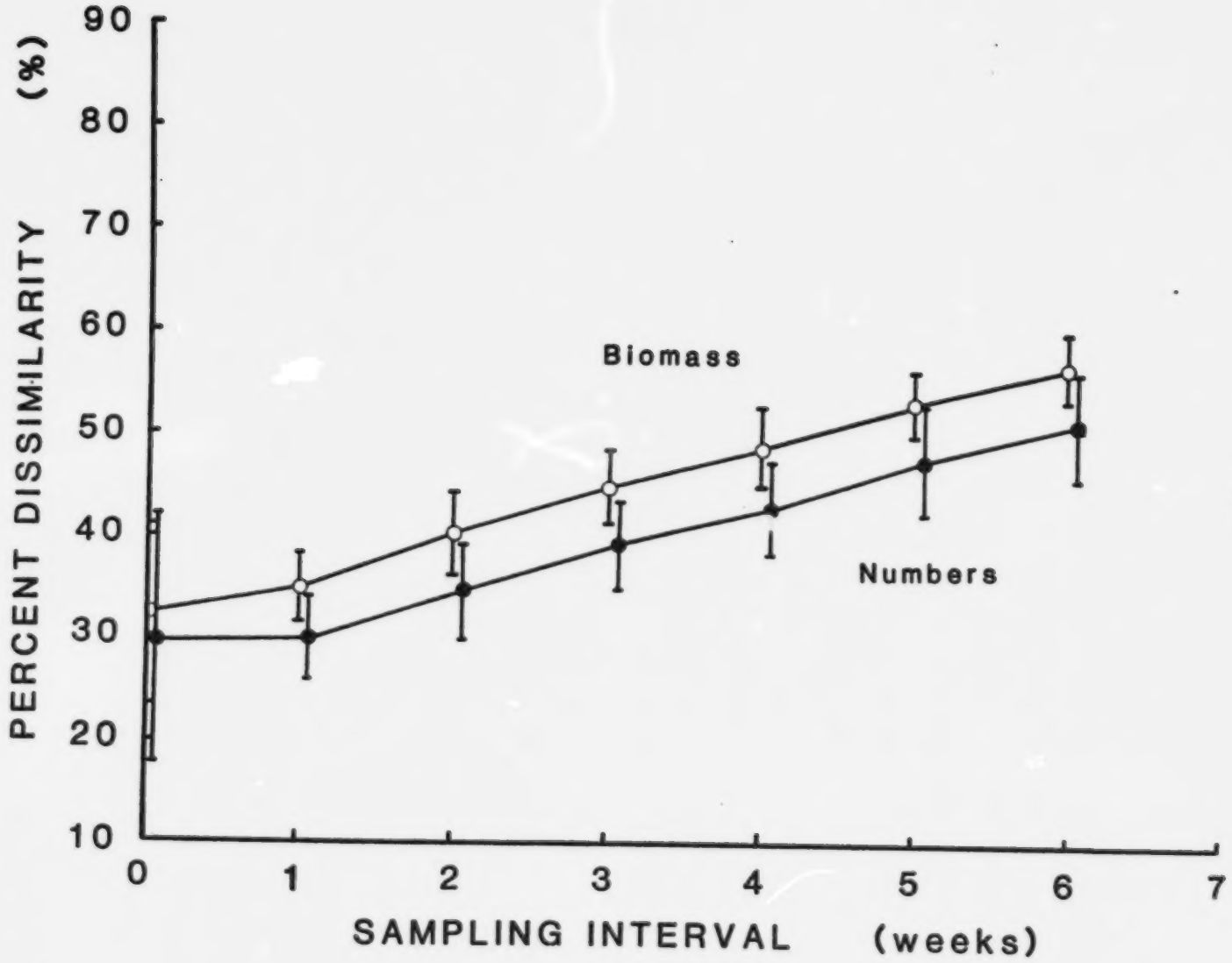

Figure 13. Percent Dissimilarity of phytoplankton communities in relation to sampling frequency.

phosphorous availability was shown to limit algal growth (Schelske and Stoermer, 1972, Schelske et al., 1972, Lin and Schelske, 1978). Examination of the historical trends in the phytoplankton data may indicate whether or not there have been changes in the algal communities which correspond with the changes in the phosphorous concentrations in the lake. Changes in phosphorous loadings can change average algal biomass, the length of periods of peak algal concentrations, and species composition (Vollenweider et al., 1974, Munawar et al., 1974, Nicholls, 1981; Tilman, 1981 and Nicholls et al., 1986).

Between 1967 and 1972 Lake Ontario phytoplankton were studied extensively (Nalewajko, 1966, 1967; Michalski, 1968; Duthie and Sreenivasa, 1971; Munawar and Nauwerck, 1971; Munawar et al., 1974; Sreenivasa and Nalewajko, 1975; and Stoermer et al., 1975). No survey work has been published since then. Unfortunately, the studies from the late 1960s, early 1970s and early 1980s are not directly comparable. Not only were the samples collected from different locations using slightly different methods and sampling intervals, but the methods of preservation, sample preparation, and counting were not uniform.

Differences in sample locations amongst the studies is not critical. Within each period (1960s, 1970s, 1980s) both inshore and offshore stations were studied. In addition, normal annual variability of phytoplankton community structure in Lake Ontario is greater than regional variability within a single year (Johannsson and Minns, in prep.).

Differences in sampling frequency may influence the results, due to the less intensive sampling frequency in the earlier studies. Important species observed in the Bioindex Project may have been missed. However, species

important in earlier studies, but not in the Bioindex Project, will actually have decreased in abundance. Amongst the studies, the different methods of preservation included Lugol's solution, formaldehyde preservation followed by sand filtration, glutaraldehyde preservation followed by membrane filtration, and an alcohol-creosote treatment. The counting techniques included both Utermöhl and Sedgwick-Rafter. In addition, different levels of magnification were used for identification. The smaller and more fragile cells may be underestimated by some of these methods (Munawar and Munawar, 1980).

The identification of some algal species is often a difficult process. To determine the comparability of the Bioindex data base with the other Department of Fisheries and Oceans' Lake Ontario data sets, and to establish a correlation between the two data sets, an inter-contractor comparison of algal identification and biomass estimates was performed on nine samples from 1982. Both contractors used the Utermöhl method of counting. The majority of differences in identification occurred within the flagellates and resulted from a combination of different philosophies (clumpers, splitters) and lack of phase contrast microscopic capability (Bioindex data set). In particular, Cryptomonas, Rhodomonas, and Ochromonas species were split much more finely by one contractor. Lack of phase contrast capability led to an underestimation of the abundance of Chrysophyceae and Cryptophyceae. Bacillariophyceaen abundance also differed slightly between contractors due to differences in the definition of a 'viable' cell.

Biomass estimates may also be contractor-specific, since the estimates are based on approximations to geometric shapes and on qualitative decisions on

the boundary of the living portion of the cell. On average, the sample biomass estimates of one contractor were 0.6 $g.m^{-3}$ higher than those of the other. Therefore, it is not possible to compare directly estimates of biomass, total numbers, or algal class composition amongst all these studies. It is possible to compare the relative importance of the larger, stronger species which survive the different techniques, and are more consistently counted and identified, such as the Bacillariophyceae, Cyanophyceae, loricated Chrysophyceae and many Chlorophyceae.

The phytoplankton communities of the late 1960s, early 1970s and early 1980s are summarized and compared in Table 11. All those species which at some time contributed five percent or more to sample biomass or were considered important by the authors (only the 1966 to 1968 studies) are included. Species which contributed 10 percent or more (Bioindex, Munawar et al. 1974), or were selected as particularly important by the authors (Munawar and Nauwerck, 1971; Stoermer et al., 1975,), are marked with three asterisks. No such judgment was possible for the 1966 to 1968 studies, and all species mentioned as abundant are included. Inspection of the table indicates that the phytoplankton communities in 1970, 1981, and 1982 had the least in common with little overlap in the dominant Bacillariophyceae, Chrysophyceae, Cyanophyceae or Chlorophyceae. The communities present in 1966-1968 and 1972 were intermediate, with dominants or representatives (1966-1968) from the two extreme communities. The dominant diatom assemblages were examined for the presence of trophic indicator species. The species were defined as meso-eutrophic, that is, those species tending towards eutrophy, and meso-oligotrophic, those tending towards oligotrophy, based on work in the

Great Lakes by Stoermer and Yang (1969), Munawar and Munawar (1980) and Nicholls (1981) (Table 12). Although the number of meso-oligotrophic species has remained relatively constant over the years varying from zero in 1970 to three in 1981 and 1982, the number of meso-eutrophic species has declined from six to nine in the earlier studies to four in 1981 and 1982 (Table 12). The ratio of meso-oligotrophic to meso-eutrophic species has changed from 0:6-2:7 to 3:4 suggesting a slight shift away from the more eutrophic community.

Further evidence of trophic changes in the algal communities in Lake Ontario is derived from algal distributions within the Great Lakes. A definite gradient in trophic conditions exists within the Great Lakes. In order of increasing trophy they are: Lake Superior, Lake Huron, Lake Michigan, Lake Ontario and the eastern, central, and western basins of Lake Erie (Patalas, 1972; Vollenweider et al., 1974). Munawar and Munawar (1981) collated all the phytoplankton studies completed on the Canadian Great lakes in the early 1970s and prepared tables of species distributions by lake. These distributions indicate which species are found predominantly in more eutrophic or oligotrophic areas and which are eurytrophic or intermediate. Changes in the trophic state of the phytoplankton community can be detected by comparing the species composition in Lake Ontario in each historical study with the distribution of the same species in the early 1970s. In order to make these comparisons the species distributions had to be categorized. All species present in Lake Erie, but not Lake Superior were considered "more eutrophic" (E), in Lake Ontario or Lake Erie and Lake Superior, "meso-eutrophic" (M), and only in Lake Huron and/or Lake Superior, "more oligotrophic" (O). The dominant species in each study were scored and tallied

TABLE 12: Historical distribution of indicator diatom species in Lake Ontario. The classification of species as being more indicative of meso-eutrophic or meso-oligotrophic conditions is based on work within the Great Lakes. Abbreviations used in the table: Stoermer and Yang (1969) = S+Y, Munawar and Munawar (1980) = M+M and Nicholls (1981) = N.

A) Number of Species in Each Trophic Classification

YEAR	MESO-OLIGOTROPHIC	MESO-EUTROPHIC
1966-68	2	9
1970	0	6
1972	2	7
1981-82	3	4

B) Classification of Indicator Species

Species	Classification	Sources
Stephanodiscus niagarae	Meso-Eutrophic	M+M,N
S. hantzschii	Meso-Eutrophic	S+Y,M+M,N
S. h. var. pusilla	Meso-Eutrophic	M+M
S. tenuis	Meso-Eutrophic	S+Y,M+M
S. alpinus	Meso-Eutrophic	S+Y
S. astrea var. minutula	Meso-Eutrophic	S+Y
Melosira binderana	Meso-Eutrophic	S+Y,M+M,N
Diatoma tenue var. elongatum	Meso-Eutrophic	M+M
Asterionella formosa	Meso-Eutrophic	S+Y
Fragilaria capucina	Meso-Eutrophic	S+Y,M+M
F. crotonensis	Meso-Eutrophic	S+Y
Melosira islandica	Meso-Oligotrophic	S+Y
Tabellaria fenestrata	Meso-Oligotrophic	S+Y
Synedra ulna	Meso-Oligotrophic	M+M

(Table 13). Again, 1970 appears to have the most eutrophic community with a ratio of O/M/E species of 0/13/7. In all the other studies there were fewer E species and more O species. This was especially marked in 1981 and 1982 when the ratio of O/M/E species was 7/8/4. The species distribution in 1981 and 1982 was significantly different from that in 1970, but not from those in 1966 to 1968 or 1972 (Table 12).

Therefore, a general comparison of the phytoplankton communities from the late 1960s until the present time suggests that the flora of Lake Ontario was slightly more eutrophic in the late 1960s and early 1970s, than in the early 1980s. However, under the higher phosphorous conditions which existed in the late 1960s and early 1970s, a range of algal communities developed. These included both the 1970 community and the more intermediate 1966 to 1968 and 1972 communities which did not show a statistically significant change from that in 1981 to 1982.

Algal biomass is a good indicator of lake trophy (Vollenweider, 1968). Munawar and Munawar (1980) have proposed a tentative scale relating seasonal mean algal biomass with trophic status. A rough comparison of average seasonal algal biomass can be made for the Lake Ontario studies conducted by personnel from the Canadian Federal Government by implementing a correction factor determined by the inter-contractor comparison. Changes in the seasonal mean algal biomasses from 2.6 to 3.3 $g.m^{-3}$ in 1970 to 1.2 to 1.8 $g.m^{-3}$ (corrected values: observed +0.6 $g.m^{-3}$) in 1981 and 1982 suggest a slight decrease in the trophic state of the lake from meso-eutrophic to meso-trophic (Table 14). It is possible that the higher values in 1970 are an artefact of monthly sampling. However, when all possible monthly sampling strategies were

TABLE 13: Classification of dominant, non-fragile species according to their distribution within the Great Lakes during the early 1970s (cf. Tables 2 and 3, Munawar and Munawar, 1981). Species were defined as "more eutrophic" if they were found in Lake Erie but not Lake Superior, "meso-eutrophic" if they were found in Lake Ontario and "more oligotrophic" if they were found only in the Upper Lakes.

Number of Dominant Species in Each Trophic Classification

Year	More Oligotrophic	Meso-Eurytrophic	More Eutrophic
1966-68	2	13	3
1970	0	13	7
1972	4	12	4
1981-82	7	8	4

1) Chi-Square comparisons indicated that the distribution of species in 1981-82 was significantly different from that in 1970(X^2 = 8.9886, 2 d.f.) but not from 1966-68 or 1972.

2) Dinobryon were classified according to protoplast volumes, not lorica volumes, in order to be comparable to previous data.

TABLE 14: Maximum, minimum, and seasonally weighted mean algal biomass from 1970 until 1982. The 1981 and 1982 data have been "corrected" by adding 0.6 $g.m^{-3}$ to the observed biomasses (see text).

LOCATION	DATE	STN	BIOMASS ($g.m^{-3}$) MAX	MIN	MEAN	TROPHIC* CLASSIFICATION
Nearshore	1970		7.20**	1.60**	3.30	Meso-eutrophic
	1972		2.72	0.21	1.23	Mesotrophic
	1981	81	3.22	0.98	1.70	Mesotrophic
		93	3.59	0.85	1.75	Mesotrophic
	1982	81	3.05	0.97	1.75	Mesotrophic
		93	2.22	0.88	1.40	Mesotrophic
Mid-lake	1970		9.00**	1.00**	2.60	Meso-eutrophic
	1972		1.73	0.18	0.69	Oligotrophic
	1981	12	2.41	0.84	1.52	Mesotrophic
		41	2.45	0.84	1.36	Mesotrophic
	1982	12	2.24	0.67	1.24	Mesotrophic
		41	2.17	0.75	1.23	Mesotrophic

* According to the classification of Munawar and Munawar (1980).
** Taken from Figure 5 of Munawar and Nauwerk (1971).

applied to the Bioindex data and the mean and 95 percent confidence intervals calculated for each station for each year, the values in 1970 fell above the 95 percentile. Extremely low biomasses were also reported in 1972 but these may be misleading. 1972 was an unusual year. The weather conditions were extremely atypical. The lake water temperature was the coldest on record (Grumblatt, 1976) and the spring extremely wet (and therefore, overcast) (Stoermer et al., 1975). The epilimnetic total phosphorous levels decreased rapidly and were more characteristic of the early 1980s than the the early 1970s (Stevens and Johannsson, unpublished data). Light limits algal growth in the spring, and phosphorus is limiting in the summer (Scavia, 1979). The low algal biomasses of 1972 probably resulted from the unusual combination of low light, low temperature, and lower phosphorous conditions.

In conclusion, a comparison of the historical phytoplankton data for Lake Ontario over the previous 15 years suggests that there may have been a change to a slightly more meso-trophic condition. However, the most important conclusion to emerge, is that the comparison of data sets must include allowances for the techniques used and difficulties involved in identifying some algal groups. The importance of inter-calibration of contractors working on the same system, and a pictorial record of the species identifications is apparent.

SECTION THREE: ZOOPLANKTON

RESULTS

A list of the zooplankton species observed during this study can be found in Johannsson et al. (1985). Only those species which contributed more than one percent to the total seasonal biomass are discussed. These are the cladocerans: Bosmina longirostis, Eubosmina coregoni, Ceriodaphnia lacustris, Daphnia retrocurva, and the cyclopoid copepods Cyclops bicuspidatus thomasi and Trophocyclops prasinus mexicanus. Calanoid copepods were never common in our samples.

The season can be divided, on the basis of temperature, into two distinct periods characterized by different zooplankton communities. Most species found in the surface waters of Lake Ontario were restricted to the warmer stratified period corresponding approximately to seasonal-thermal periods three and four used in previous analyses. These include all the cladocerans and the copepod T. p. mexicanus. In addition, the eurythermal copepod C. b. thomasi was a prominent member of the warm water community, and was the principal zooplankton of cool isothermal conditions corresponding approximately to seasonal-thermal periods one, two, and five.

In order to compare the populations between years, the period March 30th to November 17th was selected since data are available for both years and the majority of zooplankton biomass occurred during this time. The epilimnetic, seasonally-weighted mean abundance of each species per m^{-2} (SWMN) was calculated for each station for both years. The epilimnion was defined as the

mixed depth, which was determined from rates of change in water density calculated from EBT traces. This method allows a direct comparison of the total standing crop between years, independent of the seasonal timing within the years.

Average species weights were obtained from previous work on Lake Ontario (Wilson, pers. comm.) (Table 15). The numerical data has been weighted by these factors to calculate seasonally weighted mean (SWM) biomasses when comparing the relative importance of the zooplankton species in the present analyses.

Zooplankton biomasses were greater in 1982 than 1981. The SWM biomasses for the four stations increased by 30 to 144 percent, going from 0.868 to 1.711 $g.m^{-2}$ in 1981 to 1.427 to 2.226 $g.m^{-2}$ in 1982. Bosmina longirostris was responsible for the majority of the increase at stations 12, 41, and 93. D. retrocurva also increased at stations 41 and 81 and cyclopoid copepodids at stations 12, 41, and 81. Bosmina longirostris, D. retrocurva, and cyclopoid copepodids were the dominant members of the zooplankton community at all times, and together contributed 74 to 94 percent of seasonal biomass. The increase in their abundances in 1982 more than covered the loss in biomass due to decreases in cyclopoid nauplii and T. p. mexicanus adults.

Bosmina longirostris was by far the most abundant cladocera (Table 15, Figure 14). In spite of its small size, this species often dominated when the community was analyzed in terms of biomass (Table 15), contributing between 20 and 77 percent of total seasonal biomass. Cyclopoid copepodids were the other principal zooplankton form. Only at station 81 did the SWM biomass of another cladoceran, Daphnia retrocurva, equal that of B. longirostris.

TABLE 15: Seasonally weighted mean (SWM) zooplankton community biomass ($g.m^{-2}$) and species densities ($No \times 10^3.m^{-2}$) are presented for the principal species in Lake Ontario. The percentage of the total biomass contributed by each species is given in italics. Total biomasses were calculated only from these species and will underestimate total sample biomass by 0.6 to 2.4 percent.

Year	Stn	SWM Biomass	B. longirostris	D. retrocurva	C. lacustris	E. coregoni	C. b. thomasi	T. p. mexicanus	Cyclopoid Copepodites	Cyclopoid Nauplii
1981	12	0.868	119.9	32.0	8.2	4.4	26.2	17.1	181.5	112.4
			26.3	*15.5*	*1.8*	*1.1*	*9.7*	*3.4*	*39.7*	*2.6*
	41	1.001	149.2	24.9	8.0	5.8	52.1	16.3	191.8	129.8
			28.3	*10.5*	*1.5*	*1.3*	*16.7*	*2.8*	*36.4*	*2.6*
	81	1.711	184.1	87.9	22.3	33.9	57.1	45.7	301.5	209.5
			20.4	*21.6*	*2.5*	*4.4*	*10.7*	*4.5*	*33.5*	*2.4*
	93	1.023	260.9	32.1	14.5	3.3	15.4	10.4	136.5	161.5
			48.1	*13.2*	*2.7*	*0.7*	*4.8*	*1.7*	*25.3*	*3.2*
1982	12	2.120	727.4	16.1	1.8	3.0	33.9	1.9	281.5	66.9
			65.2	*3.2*	*0.2*	*0.3*	*5.1*	*0.1*	*25.2*	*0.6*
	41	1.427	281.3	52.2	25.9	6.9	36.6	6.7	243.4	88.9
			37.5	*15.4*	*3.4*	*1.1*	*8.2*	*0.8*	*32.4*	*1.2*
	81	2.226	189.1	126.1	30.8	43.8	119.7	16.0	393.9	118.3
			16.1	*23.8*	*2.6*	*4.3*	*17.2*	*1.2*	*33.6*	*1.1*
	93	1.867	757.9	11.6	16.6	3.0	18.5	2.2	138.9	65.7
			77.1	*2.6*	*1.7*	*0.4*	*3.2*	*0.2*	*14.1*	*0.7*
*Weight per Individual (µg)			1.9	4.2	1.9	2.2	3.2	1.7	1.9	0.2

*Weights are estimates of adult body size, taken from the unpublished data of B. Wilson (per. comm.) and are presented solely to illustrate the relative size of the species.

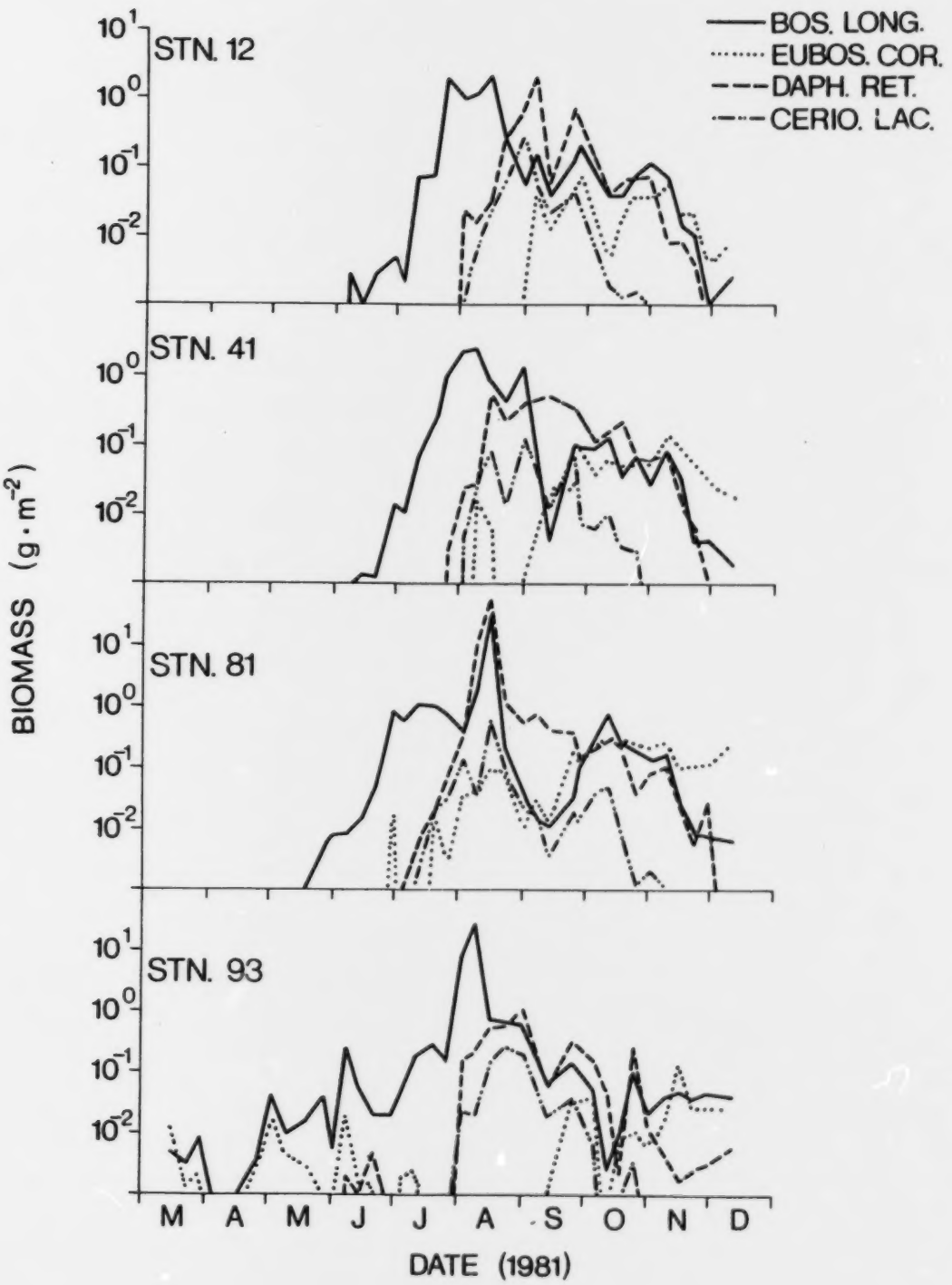

Figure 14. Seasonal trends in cladoceran populations in the epilimnion of Lake Ontario.

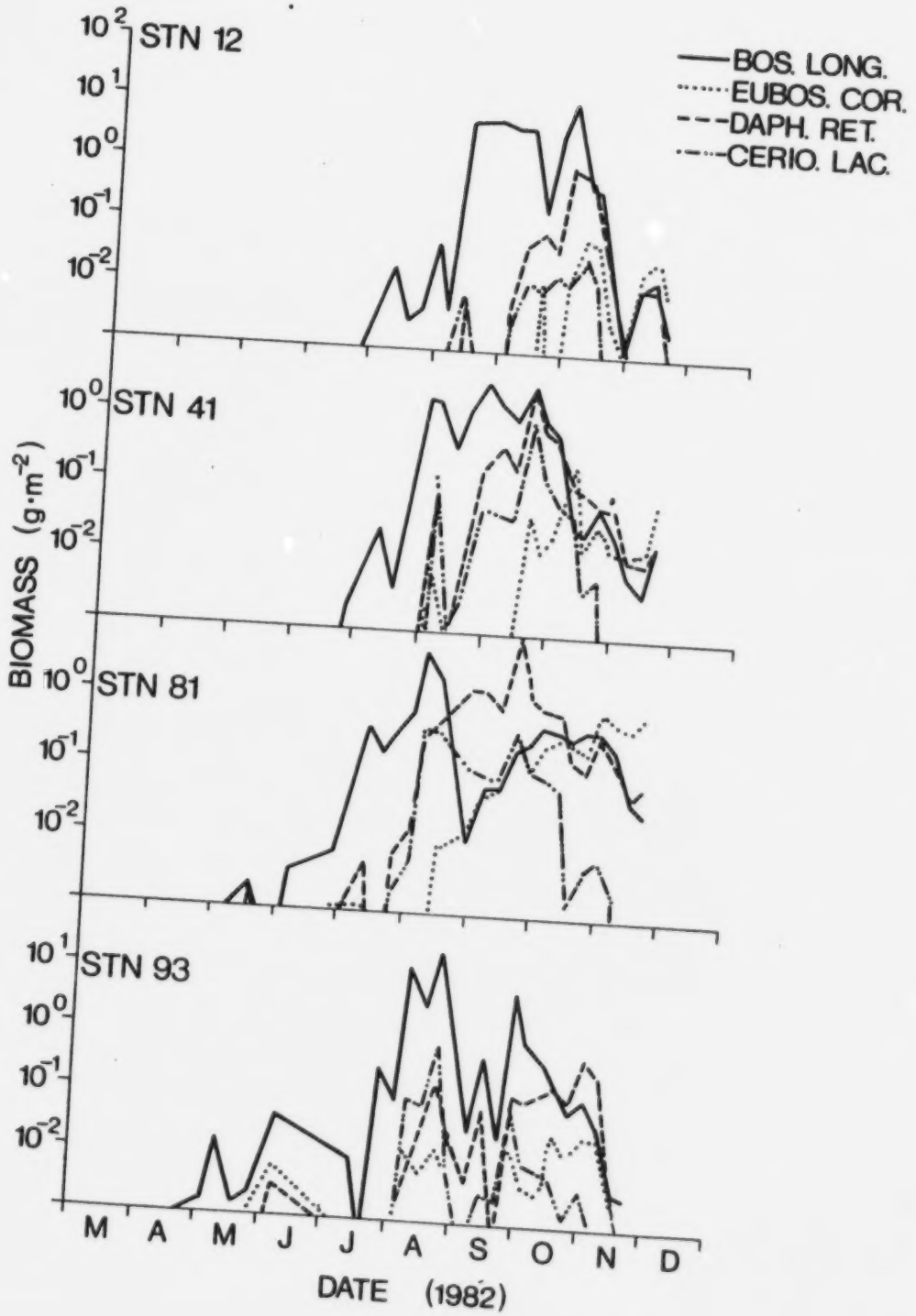

Figure 14. Continued

The Bosmina longirostris population was the first of the cladoceran populations to expand in the summer (Fig. 14). It increased rapidly in June and July, and could produce peak populations from the end of July until October. Maximum densities usually occurred in July and August and ranged from 91 to 620 x $10^3.m^{-3}$ (Table 16). These high population levels could be maintained into October (e.g., the mid-lake stations 1982), or they could be followed by a sharp decline and subsequent population peaks at reduced levels. Numbers decreased markedly in November. The B. longirostris populations were strikingly different in 1981 and 1982. The SWMN's ranged from 119.9 to 260.9 x $10^3.m^{-2}$ in 1981 and from 189.1 to 757.9 x $10^3.m^{-2}$ in 1982. The population increases were greatest at stations 12 and 93, with six- and three-fold increases respectively. The population at 41 doubled, and at 81 it remained unchanged. Table 16 and Figure 14 indicate that the marked increases at 12 and 93 resulted from a combination of larger peak densities and a delay in population decline in the fall. The peak population was actually lower in 1982 at station 41, but was compensated for by a longer period of high population levels. At station 81, the reverse occurred; the peak populations were indeed higher in 1982, but the period of high population levels was reduced due to a late start in the spring.

Daphnia retrocurva was the second most important cladoceran both numerically and because of its larger size. It contributed between 2.6 to 23.8 percent of seasonal biomass (Table 15). The D. retrocurva population started to grow rapidly in July or early August, one to two months after B. longirostris and peaked in August and September at populations of 125 to 2058 x $10^3.m^{-2}$. Maximum densities ranged from 8.2 to 108 x $10^3.m^{-3}$.

TABLE 16: Maximum population densities (No. x $10^3.m^{-3}$) attained by the dominant zooplankton species in 1981 and 1982.

Year	Stn	B. longirostris	D. rectrocurva	E. coregoni	C. lacustris	T. p. mexicanus	C. b. thomasi
1981	12	155	22	1.5	9.0	4.0	10.
	41	247	18	5.9	1.9	4.6	25.
	81	91	16	7.4	17	19.	15.
	93	250	13	1.0	11	4.4	7.2
1982	12	538	13	1.8	0.9	1.9	11.9
	41	166	40	6.7	27	2.8	9.0
	81	131	108	18	12	5.4	15.0
	93	620	8.2	1.3	21	1.2	14.

Because of its larger size, its biomass often equalled or surpassed that of B longirostris at this time. It decreased in step with B. longirostris through the autumn.

The SWMN of D. retrocurva increased at stations 41 and 81 in 1982 over 1981 by 110 and 43 percent respectively, and decreased at stations 12 and 93 by 50 and 64 percent respectively. The patterns in peak biomass were similar, but the increases were more extreme: 2.5-fold (station 41) and 7-fold (station 81). In all instances the populations started to increase several weeks later in 1982 than in 1981; only at stations 41 and 81 was the late start compensated for by larger population densities.

Ceriodaphnia lacustris was a minor element of the zooplankton community, contributing 0.2 to 3.4 percent of the seasonal biomass. Its populations started to increase at the same time as those of D. retrocurva, and also peaked in August and September, although they could extend into October. The peaks reached 19 to 537 x $10^3.m^{-2}$ and the maximum densities ranged from 0.9 to 27.0 x $10^3.m^{-3}$. They declined in October, noticeably earlier than the other cladocerans. The SWMN of C. lacustris differed between years. In 1982 it was more abundant at stations 41 and 81 than in 1981, 25.9 and 30.8 x $10^3.m^{-2}$ as compared with 8.0 and 22.3 x $10^3.m^{-2}$. It remained unchanged at 14.5 to 16.6 x $10^3.m^{-2}$ at station 93, and decreased from 8.2 to 1.8 x $10^3.m^{-2}$ at station 12. These differences were the result of both differences in peak densities and seasonal patterns of growth. For instance, the peak density at station 41 was low in 1981, 1.9 x $10^3.m^{-3}$, and high in 1982, 27.0 x $10^3.m^{-3}$. However, the SWMN did not change to the same extent because the growing season in 1982 was shorter than in 1981.

Eubosmina coregoni, like C. lacustris, was a minor element of the zooplankton community. At the mid-lake stations its numbers increased rapidly at the end of August or early September. Major peaks of 31.7 to 36.7 x $10^3.m^{-2}$ (station 12) and 62.8 to 134.4 x $10^3.m^{-2}$ (station 41) were observed in September. The populations remained high until sampling ceased in mid-December (1981) or late November (1982). Maximum population densities ranged from 1.5 to 6.7 x $10^3.m^{-3}$. At the nearshore stations, small population increases were observed from May to July. The main population peak however, occurred in August or September and continued until sampling ceased. Peak populations ranged from 15.0 to 20.1 x $10^3.m^{-2}$ at station 93 to 149.4 to 153.0 x $10^3.m^2$ at station 81. Maximum population densities ranged from 1.3 to 18.0 x $10^3.m^{-3}$. The SWMs in both years were similar (falling within 25 percent of each other) and ranged from 3.0 to 43.8 x $10^3.m^{-2}$.

Cyclops bicuspidatus thomasi was the dominant cyclopoid. A representative example of the population dynamics of this species is presented in Figure 15, where the number of adults, eggs, cyclopoid nauplii and cyclopoid copepodids are plotted for one season. Cyclopoid nauplii and copepodids were not identified to species. Similar data for the other stations and years are available in Johannsson et al. (1985).

In March the surface water zooplankton community was depauperate, and consisted of low numbers of adults, nauplii, and copepodids. Sometimes small copepodid peaks were observed very early in the spring. These rapidly disappeared as the number of adult C. b. thomasi and eggs increased, once in April/May and again in June/July. The associated peak in nauplii usually occurred in late May to early June. The first copepodid peak followed or overlapped the peak in nauplii.

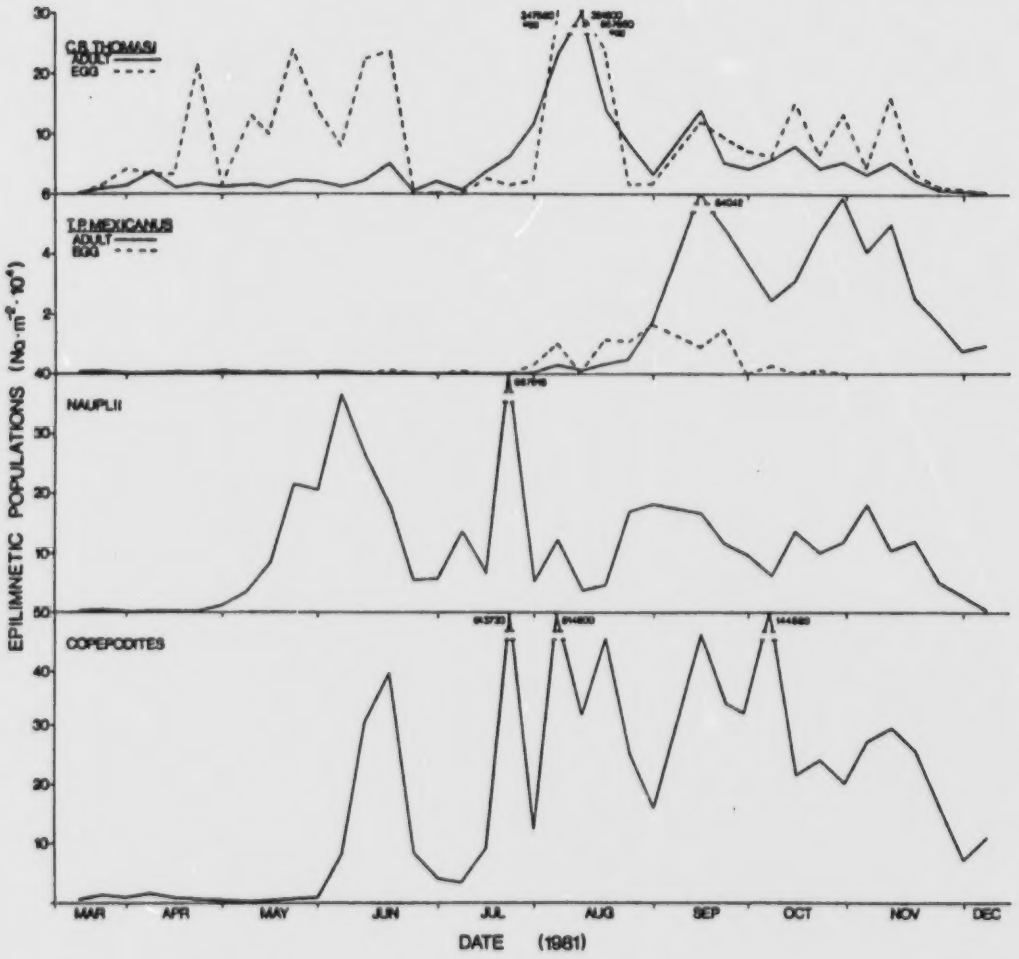

Figure 15. Seasonal trends in cyclopoid populations in the epilimnion of Lake Ontario, showing adult and egg numbers of Cyclops bicuspidatus thomasi and Tropocyclops prasinus mexicanus, and total cyclopoid copepodid and naupliar numbers. Station 41,1981.

Often in July only very low numbers of adults, nauplii, and copepodids were found, presumably due to the shallowness of the epilimnion. Major peaks in C. b. thomasi adults occurred from August until October. Usually maximum populations were attained in August to September, but on occasion the August peak was small relative to the September to October peaks (e.g., 1982, mid-lake stations). Egg production was roughly related to adult population size and continued at least until the end of November or early December when sampling ceased. As of July the nauplii and copepodids consisted of numerous individuals of T. p. mexicanus as well as C. b. thomasi, masking the development of both species. Peaks in nauplii continued to follow peaks in egg production; and peaks in copepodids, followed those in nauplii, although they were somewhat indistinct.

The SWMN of C. b. thomasi ranged from 26.2 to 52.1 x $10^3.m^{-2}$ at the mid-lake stations, 15.4 to 18.5 x $10^3.m^{-2}$ at station 93, and 57.1 to 119.7 x $10^3.m^{-2}$ at station 81. Although the SWMN's were greater in 1982 than 1981 at stations 12 and 93, the contribution of C. b. thomasi to seasonal zooplankton biomass decreased by approximately 50 percent; in 1982 it contributed 3.2 to 5.1 percent as compared with 4.8 to 9.7 percent in 1981. At station 41 both the SWMN and percent of biomass decreased by 20 to 50 percent, while at station 81 they increased by 70 to 100 percent.

Trophocyclops prasinus mexicanus, the other important cyclopoid, is a small eurythermal species. It did not appear in the plankton in any numbers until May or June nearshore, and June or July mid-lake. Normally a series of adult population peaks occurred across the remainder of the season. There were usually four to five peaks with concurrent egg production, though this varied

from two (station 12, 1982) to eight (station 81, 1981). Maximum populations were attained in September and October just prior to the cessation of egg production in mid-October. The maximum populations ranged from 20 x $10^3.m^{-2}$ at station 12 in 1982 to 398 x $10^3.m^{-2}$ at station 81 in 1981.

Trophocyclops prasinus mexicanus was more important at station 81 than at any of the other stations. It contributed 1.2 and 4.5 percent to seasonal biomass and had SWMN of 16.0 and 457 x $10^3.m^{-2}$ in 1982 and 1981 respectively. In 1982 it was also less abundant at the other stations than in 1981. The SWMNs dropped from 10.4 to 17.1 x $10^3.m^{-2}$ to 1.9 to 6.7 x $10^3.m^{-2}$, and the biomass contribution fell from 1.7 to 3.4 percent to 0.1 to 0.8 percent

The Cyclopoid copepodids, as a group, were more important than either of the adult cyclopoids and were a significant component of the zooplankton community. In 1981 they were more important, both numerically and in terms of biomass, than any other component, with the exception of B. longirostris at station 93. That year copepodids contributed 25.3 to 39.7 percent to seasonal biomass, had SWMNs of 136 to 301 x $10^3.m^{-2}$ and reached peak populations of 684 to 874 x $10^3.m^{-2}$. Although they were 27 to 55 percent more abundant in 1982 at all stations except 93, their contribution to seasonal biomass decreased, at all stations except 81, by 11 to 44 percent due to marked increases in B. longirostris at stations 12, 41, and 93, and D. retrocurva at stations 41 and 81.

DISCUSSION

SAMPLING

The observed zooplankton community structure and species densities can be affected by sampling methodology. The vertical distribution of each zooplankton species is unique, varying both diurnally and seasonally: if only a portion of the water column is sampled, the population dynamics and densities observed can be affected by vertical population structure. The vertical distributions of zooplankton in the Great Lakes have been studied by Wells (1960, 1970), McNaught (1966), Carter (1969), Patalas (1969), Wilson and Roff (1973) and Fricker and Abbott (1984). The work of Wilson and Roff is of particular importance because they studied both seasonal and diurnal changes in distribution. Judging by the information presented in these papers, the Bioindex sampling program is adequate for some species, but not all.

Bosmina longirostris, E. coregoni, C. lacustris and, to a lesser extent, D. retrocurva, T. p. mexicanus, and Diatomus minutus, are restricted to warm water during stratified conditions and consequently are well sampled at this time. Although D. retrocurva is found principally in the epilimnion, many individuals move through the thermocline during diurnal migrations reaching maximum depths in late afternoon. Samples were, for the most part, collected during the day at stations 12, 81, and 93 and during the night at station 41. Therefore, D. retrocurva may be underestimated at stations 12, 81, and 93. Cladocerans are only abundant during stratified conditions and therefore are well sampled by epilimnetic sampling. Copepods are abundant all year in Lake

Ontario. During unstratified periods T. p. mexicanus and D. minutus are spread diffusely through the water column with mean population depths of 40 to 60 m and 40 to 50 m respectively (Wilson and Roff, 1973). During stratified conditions they are restricted to the epilimnion, and should be adequately sampled all year.

Diatomus sicilis and Limnocalanus macrurus are restricted to the hypolimnion and are always greatly underestimated.

Cyclops b. thomasi, Diatomus oregonensis, and Eurytemora affinis occupy intermediate positions. During isothermal conditions they are diffusely spread through the water column. During stratified conditions the C. b. thomasi population is centred in the lower epilimnion, E. affinis, just below this and D. oregonensis, in the metalimnion. These positions are fluid with diurnal migrations toward the surface at night and down during the afternoon. Therefore C. b. thomasi, E. affinis, and D. oregonensis are never accurately sampled, but the estimates are better during stratified than unstratified conditions.

In spite of the sampling deficiencies, epilmnetic data can be used to compare species abundances across years, assuming that the relative proportions of the populations within the sampled depth range are constant. However, the present method samples only very small proportions of the populations of hypolimnetic species in isothermal periods, and will be sensitive only to large changes in their densities. Thus, even for monitoring purposes, regular hypolimnetic sampling should be added to the program. Addition of hypolimnetic samples would also permit better estimates of population densities and more accurate estimates of production of copepods.

These data are particularly valuable in interpreting the interrelationships among phytoplankton, herbivorous zooplankton, predaceous zooplankton, and other zooplankton predators.

The principal physical factor affecting the accuracy of zooplankton samples is the decrease in filtering efficiency as the net clogs. The rate of clogging is dependent on the type and amount of seston in the water. Therefore, efficiency will vary seasonally and with the length of tow. A study of net efficiency is needed to improve the quality of the zooplankton data.

LIFE HISTORY PATTERNS

Between 1967 and 1972 several whole-lake, long-term studies of Lake Ontario zooplankton communities were conducted by the Canadian and American governments (Patalas, 1969; Watson and Carpenter, 1974; Czaida, 1974, 1978; McNaught et al., 1975). These studies identified the dominant species, tracked their population developments over the year and determined lake-wide densities. The findings of these studies were similar to those of the present study. In all instances the community was dominated by B. longirostris, D. retrocurva, C. lacustris, E. coregoni, T. p. mexicanus, and C. b. thomasi. Calanoid and harpacticoid copepods were never abundant, but Eurytemora affinis, Diatomus sicilis, D. oregonensis, D. minutus and Limnocalanus macrurus were caught in all studies.

The life histories of most dominant species are simple. The Cladocera and the copepod, T. p. mexicanus are warm-water, epilimnetic species which reproduce rapidly, producing many generations in one season. Their

populations increase exponentially, reaching maximum densities during the late summer or autumn. Cyclops b. thomasi, however, is a larger species with a slower growth rate. It's life history was determined by Torke (1975) in Lake Michigan. The temporal patterns of adult abundances are similar in both lakes, and therefore the life histories are believed to be the same. The species overwinters principally in the copepodid stage and matures to the C6 (adult stage) early in the spring. The offspring (G1) grow rapidly and mature in July/early August. Torke concluded that some of the offspring of this mid-summer population (G2) reached adulthood by late summer and produce a G3 generation. The majority, however, overwinter as copepodids. Thus, the offspring of the fast-growing G2 population would overwinter with the slow growing G2 individuals to form the adult population next spring. In Lake Ontario the data suggests two pre-summer peaks in adult numbers and egg production (April to May, June to July). This may mean that the G2 and G3 offspring mature at different times in Lake Ontario. The development of the offspring from these two groups would tend to merge to form the August/September peak. Egg and larval development times are related to temperature (Torke, 1975). At water temperatures of 3°C, as would occur in April/May, C. b. thomasi eggs require 500 h (20.7 d) to develop, while at 13°C, a June temperature, they would take 116 h (4.8 d) (Borgmann et al., 1984). The blurring of peaks from August to October/November may be due to incomplete merging of the offspring of the two overwintering generations and a fast-growing G2 population.

TRENDS SINCE 1967

The first comprehensive survey of Lake Ontario zooplankton was conducted in 1967 by Patalas (1969), who monitored zooplankton abundance monthly at 32 stations covering the entire length and width of the lake. Watson and Carpenter (1974) conducted a similar survey in 1970, and McNaught et al. (1975) in 1972. Czaida (1974, 1978) studied inshore - offshore trends through the season of 1972 along the southern shore of the lake. All studies used fine-meshed conical nets (64 μ or 77 μ) pulled vertically through the water column. The nets varied in diameter from 0.25 m to 0.80 m. The sampling depth in 1967 and 1970 was 0 to 50 m; in 1972 however, it was 0 to 5 m in the whole-lake study and surface to bottom in the south shore work. The top five meters does not adequately represent the zooplankton community (Fricker and Abbott, 1984), therefore, only the southshore work from 1972 has been included in the comparison.

Since Patalas (1969) found over 90 percent of most species in the top 50 m, bottom to surface (1972) and 0 to 50 m (1967, 1970) tows are comparable. Epilimnetic or 0 to 20 m hauls, however, are likely to sample some populations more adequately than others. In 1982 Fricker and Abbott (1984) took bottom to surface tows at a station (403) only 10 km east of station 41, allowing epilimnetic and total column sampling to be compared. Zooplankton population development is closely associated with temperatures which has a seasonal east-west gradient in Lake Ontario (Patalas, 1969, 1972). Therefore, it is inappropriate to compare data from the same sampling dates. Peak population densities at the two stations were compared instead (Table 17). Peak populations of B. longirostris, E. coregoni, and D.

TABLE 17: A comparison in epilimnetic and whole-column water samples for the dominant zooplankton species. The peak populations are reported for 1982 at Stations 41 (Bioindex) and 403 (Fricker and Abbott, 1984).

Species	Number/m^2 x 10^2 Stn 41 (epilimnetic)	Stn 403 (whole-column)	Percent (E/WC)
Bosmina longirostris	18,313	23,040	79
Eubosmina coregoni	1,344	1,920	70
Ceriodaphnia lacustris	5,375	3,350	160
Daphnia retrocurva	2,914	3,280	89
Trophocyclops prasinus mexicanus	565	880	64
Cyclops bicuspidatus thomasi	1,599	5,520	29

retrocurva at station 41 were 75, 70, and 89 percent of the Fricker and Abbott densities, respectively, while C. lacustris was 60 percent higher. As expected, the copepods, especially C. b. thomasi, were underestimated by epilimnetic sampling. The T. p. mexicanus peak at 41 was 64 percent of that at 403, and the C. b. thomasi peak, 29 percent. The results indicate that the cladoceran and T. p. mexicanus abundances are roughly comparable among studies and that C. b. thomasi was underestimated in the epilimnetic samples by a factor of 3.1.

In order to compare zooplankton composition and abundance across years, the June to October data from each study were averaged as per the 1967 study (Patalas, 1969). Hypolimnetic zooplankton were excluded from the analyses since they were poorly sampled in 1981 and 1982 and constituted only a small proportion to zooplankton abundance during this period of the year (Patalas, 1969). The 1970 composite figures were derived from the raw data (Watson, personal data), and not from published numbers (Watson and Carpenter, 1974) because mean sampling depth was not given in the published work. In 1972 only the 8 km offshore data (Czaida, 1974) were used in order to avoid nearshore effects. These data were converted from density (Czaida, 1974, Table 1) to numbers $.m^{-2}$ by multiplying by the mean station depth, 85 m. The 1982 data were split into western (12, 93) and eastern (41, 81) sections since the zooplankton communities differed greatly between the two ends of the lake.

The effects of spatial sampling patterns were examined using Watson's 1970 raw data. Zooplankton abundance and sub-order composition were compared amongst three data subsets: whole lake (all stations-comparable with the 1967 and 1970 studies), south shore (three stations - the 1972 study), and Bioindex locations (four stations - the 1981 and 1982 studies). Since the three data

sets provided similar results (Fig. 16), the different spatial sampling patterns employed in different years should not affect the historical comparisons.

Average summer zooplankton abundance varied greatly between 1967 and 1982 with minimum levels of $10 \times 10^5 .m^{-2}$ observed in 1970 and 1972 (Fig. 16), and maximum levels of $30 \times 10^5 .m^{-2}$ in 1967 and 1982. Abundance in 1981 was intermediate.

The differences in abundance may have been due to less frequent sampling of the earlier studies. However, the abundances of zooplankton in 1981 and 1982, calculated with the Bioindex data and assuming all possible monthly sampling strategies, were significantly greater than the abundances in 1970 and 1972 (Table 18). The proportion of the zooplankton community composed of Cladocera also changed during this time. Cladocera formed 40 to 50 percent of the community in 1967, 1970, and 1982 (west), but only 18.8 to 21.8 percent in 1972, 1981, and 1982 (east)(Fig. 16). Cladoceran abundances were similar in 1970, 1981, and 1982 (east) ranging from 387×10^3 to $684 \times 10^3 .m^{-2}$. A lower value ($187 \times 10^3 .m^{-2}$) occurred in the unusually cold year 1972 (Stoermer et al., 1975; Grumblatt, 1976). In 1967 and 1982 (west) the abundances were 1294×10^3 and $1477 \times 10^3 .m^{-2}$ respectively. Thus, changes in cladoceran abundance were not tightly correlated with changes in total zooplankton abundance.

The composition of the cladoceran community has remained relatively unchanged from 1967 to 1982 (Table 19). Bosmina longirostris constituted 53.9 to 74.1 percent of the community, D. retrocurva (Daphnia spp. 1970) 21.2 to 28.5 percent, C. lacustris 4.2 to 13.2 percent, and E. coregoni 2.6 to 7.5 percent (Fig. 17). Thus, within this time period, community structure and

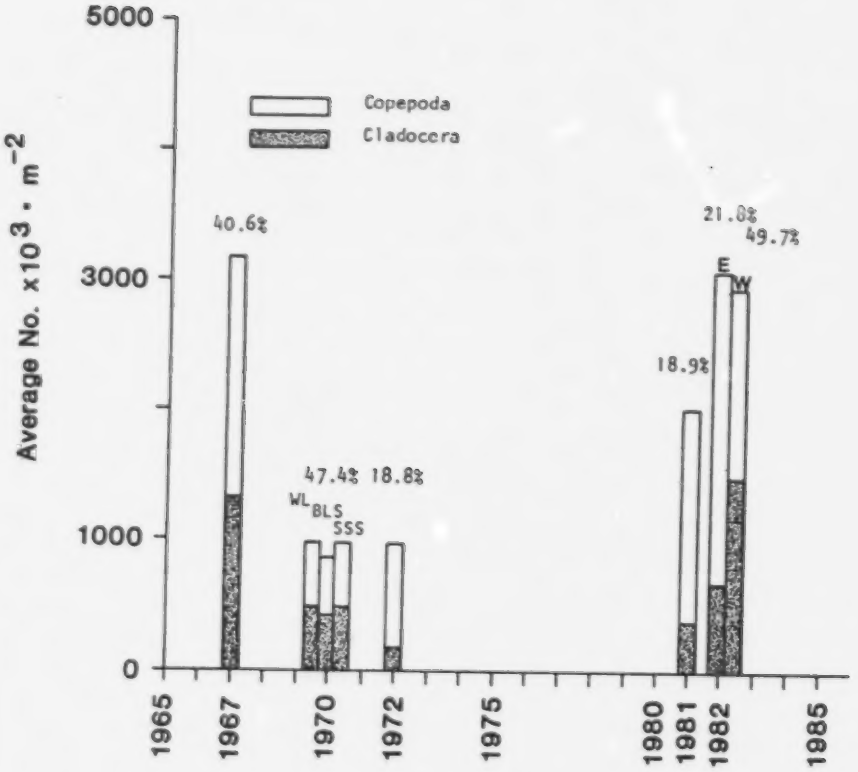

Figure 16. Average Lake Ontario June to October zooplankton abundance for studies from 1967 to 1982. The percentage of Cladocera is given above the bar. WL = whole lake, SSS = south shore subsample, BLS = Bioindex locations subsample, E = eastern region, W = western region.

TABLE 18: Estimates of average zooplankton abundance between June and October from 1967 to 1982, assuming various monthly sampling strategies in 1981 and 1982.

Year	Mean ($No.m^{-2}$)	S.D.	95% Confidence Interval
1967	3,186		
1970	832		
1972	996		
1981	1,995	±484	1,027 - 2,963
1982	2,792	±702	1,388 - 4,196

TABLE 19: Percent similarity of cladoceran and copepod communities based on proportionate data.

	YEAR							
C	1967	-						
L	1970	92.5	-					
A	(1970-BS)	88.1	93.7	-				
D	1972	89.2	82.5	81.6	-			
O	1981	84.6	92.8	96.3	78.3	-		
C	1982E	92.2	93.7	92.2	88.6	89.4	-	
E	1982W	62.8	70.4	74.7	57.1	77.3	66.9	-
R								
A								
		1967	1970	1970-BS	1972	1981	1982E	1982W
C	1967	-						
O	1970	84.8	-					
P	(1970-BS)	92.9	91.9	-				
E	1972	86.0	98.8	93.1	-			
P	1981	97.3	87.5	95.6	88.7	-		
O	1982E	87.6	72.4	80.5	73.6	84.9	-	
D	1982W	84.5	69.3	77.4	70.5	81.8	96.9	-
A								

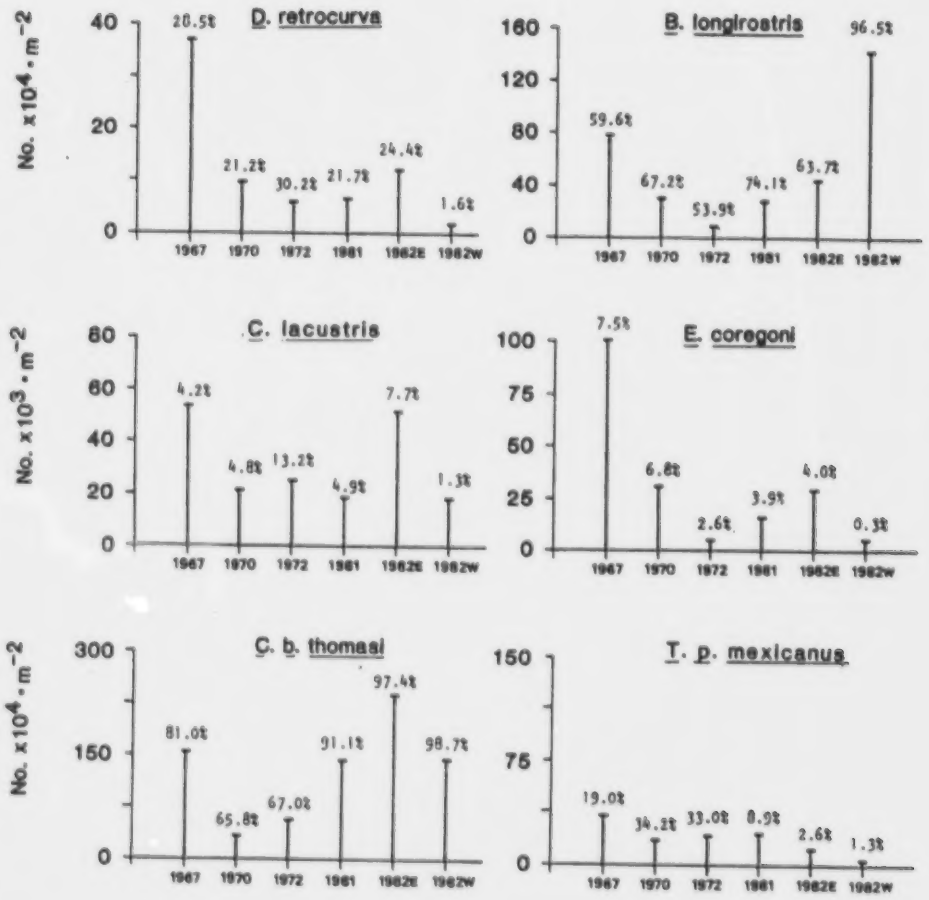

Figure 17. Average June to October abundance and percentage composition of the dominant zooplankton species for studies from 1967 to 1982. See text concerning reasons for dividing the lake in 1982. E = eastern region, W = western region.

total abundance are independent. In the western portion of Lake Ontario in 1982, an extreme version of the normal community developed (Table 19). Daphnia retrocurva, C. lacustris and E. coregoni were virtually eliminated, while B. longirostris increased dramatically in abundance and percent composition (Fig. 17).

Although cladoceran community structure was not related to total zooplankton abundance, copepod structure was correlated with it. The abundance of C. b. thomasi rose disproportionately with increases in zooplankton abundance, so that it formed 81 to 96 percent of the copepod community when zooplankton were abundant, and only 65 to 67 percent when they were not. Trophocyclops p. mexicanus abundance did not change or may have decreased during this time; the data are inconclusive.

With the exception of the western portion of the lake in 1982, cladoceran community structure has been stable since the late 1960s. Do the changes in 1982 signify a significant change in the structuring/functioning of the zooplankton community in the lake? Zooplankton community structure and abundance are determined by the trophic status of a lake, predation pressures from vertebrates and invertebrates, competition, and physical factors (Brooks and Dodson, 1965; Brooks, 1969; Patalas, 1972; Lane, 1978, 1979; Lynch, 1979; Ravera, 1980). Patalas (1969) showed that the peak standing stock of D. retrocurva was closely related to the surface water (0 to 25 m) heat content. The summer of 1982 was cool and upwelling events were common in the western end of the lake. A logarithmic plot of D. retrocurva abundances in 1981 and 1982 vs cumulative epilimnetic temperature showed that population growth was closely related to cumulative temperature at each station

(Fig. 18). The differences observed between years in D. retrocurva abundance were due to differences in the thermal regimes within these years. Therefore, when D. retrocurva had to grow only at cooler temperatures (≃15°C) in 1982, the population became abundant much later in the year and contributed less to total zooplankton standing stock than in 1981 when the population grew in warmer water (≃19 to 20°C). Bosmina longirostris became extremely abundant under these cool conditions, and may have been released from competitive pressure with D. retrocurva for food. The larger Daphnia are known to out compete the smaller zooplankton.

The marked increase in B. longirostris may also suggest a release from predation pressure. The alewife, Alosa pseudoharengus, is the principle epilimnetic predator, and feeds heavily on zooplankton (Scott and Crossman, 1973). Alewife distribution is skewed toward higher temperatures in summer (Olson, 1984), thus the alewife may have moved across the lake with the warmer water during the 1982 upwelling events. Alternately, the lower temperatures may have encouraged a greater overlap of the salmonids and alewife populations, resulting in increased mortality and a consequent decreased abundance of alewives in the upwelling areas. The hypothesis of decreased alewife abundance is supported by the relative increase in Daphnia galeata mendotae and Daphnia longiremis in the western end of the lake as compared with the eastern portion. These two larger cladocerans are selectively eaten by alewife (Brooks and Dodson, 1965).

The proportion of copepods, principally C. b. thomasi, in the zooplankton community increased from 50 to 60 percent in 1967 and 1970, to 80 percent in 1972. Copepod abundance, however, did not increase until the early 1980s. The switch in proportions in 1972 may have been due to the exceptionally cold weather conditions that year. Cladoceran population growth is highly

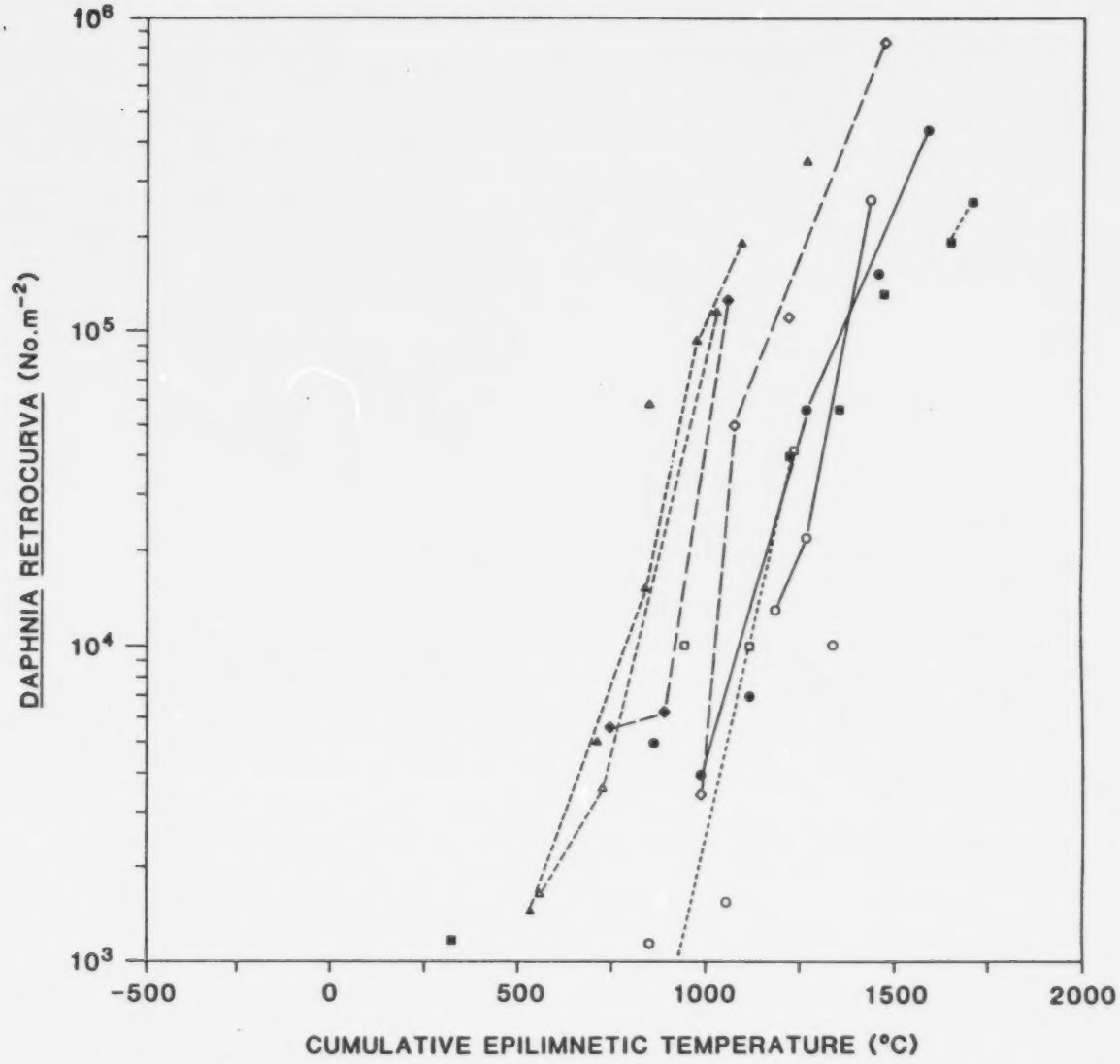

Figure 18. Relationship between Daphnia retrocurva population growth and cumulative epilimnetic temperature. Solid symbols = 1981, open symbols = 1982, stn 12 = ○—○, stn 41 = ●-□, stn 81 = △----△, stn 93 = □----□.

dependent on temperature. Reduced growth rates without a decrease in predation pressure may have been responsible for the very low cladoceran standing stocks, and consequently higher proportion of copepods, observed that year. However, the persistence of the change in copepod proportion into the early 1980s suggests that other factors were important, at least in the latter years. During the 1970s, Lake Ontario experienced both a 50 percent decrease in phosphorous loading (Stevens and Neilson, in prep.) and a massive salmonid stocking program (Kolenosky and Le Tendre, 1984). Salmonid predation could affect the zooplankton community through effects on the abundance and/or distribution of planktivores. In the summer, salmonid distributions are centred in or near the thermocline (Lichorat, 1982; Olson, 1984). Increased predation pressure in the metalimnion may have reduced the abundance of zooplankton predators in this region. Cyclops b. thomasi would benefit more than the other zooplanktors from this more favourable environment. Therefore, the increases in the C. b. thomasi populations in the 1980s may be due to increased salmonid predation pressure on planktivores in the metalimnion. Since salmonid abundance in the epilimnion is much lower, salmonids may have little or no effect on predator-prey relationships in the epilimnion, with the exception of the indirect effect of the increased C. b. thomasi abundance. Conditions in the epilimnion have been and still are dominated by predation pressure of alewives on zooplankton. Three lines of evidence support this hypothesis. First, the preponderance of small cladocerans in the community is symptomatic of a zooplankton assemblage structured by intense fish predation (Brooks and Dodson, 1965). Second, the very low condition factor of alewives caught in the autumn from 1981 to 1984 (O'Gorman, pers. comm.) suggests that

the population is food limited and at its carrying capacity (O'Gorman, and Sneider, 1986). Third, Christie (1974) reported that alewife populations have had a continuous history of boom-bust population dynamics in Lake Ontario since the turn of the century, consistent with non-predatory population control: the most recent die back was in 1984 (O'Gorman per. comm.).

This scenario of a proportionate change in alewife vertical distribution would lead to an increase in the proportion of copepods in the population, as was observed in the early 1980s. Interestingly, when epilimnetic predation pressure was reduced in the western portion of the lake in 1982 and cladoceran abundance increased dramatically (see above), the proportion of copepods dropped to the level observed prior to 1972. The metalimnetic salmonid predation hypothesis is supported by several lines of evidence in addition to the biological changes observed during upwelling events in Lake Ontario in 1982. Salmonids in Lake Ontario are known to be vertically distributed about the thermocline (Olson, 1984); lake trout and brown trout, in particular, feed on alewife (Olson, 1984). The alewife's thermal distribution is flexible and responsive to biological pressures: in Lake Michigan alewife distribution changed between 1977 and 1979 in response to increased competition with an expanding bloater population (Coregonus hoyi) (Brandt et al., 1980; Crowder and Magnuson, 1982). In Lake Ontario the alewife population distribution in 1982 was skewed towards higher temperatures with maximum abundances near 22°C (Olson, 1984). Less than ten percent of the population was found in or below the thermocline (Olson, 1984). The evidence is not conclusive, but suggests that salmonids may be affecting the zooplankton community in a subtle fashion.

SECTION FOUR: BENTHIC FAUNA

RESULTS

Since the benthic studies were temporarily dropped in 1984, the 1981 to 1983 results are dealt with as a unit in this report.

Because of the importance of Pontoporeia to the energetics of Lake Ontario, the main aim of the benthic sampling was to examine population size and growth rates of this species at the sample sites. Although populations of Pontoporeia are high at station 93 (18 m) during the spring and fall, the development of summer stratification at that depth results in bottom temperatures in excess of the tolerance of adult Pontoporeia (15°C; Dadswell, 1974). The temperature tolerance of the species required the collection of samples from depths below 30 m. A deposition zone of decaying leaves and debris from the Niagara plume existed at a depth of 30 to 50 m eastward from the Niagara River to station 93. As a result, high numbers of tubificid worms (7040 m^{-2}) but low populations of Pontoporeia existed at this depth. The samples at the Niagara station were collected further offshore at 70 m depth, in order to ensure adequate numbers of Pontoporeia with which to analyze their population dynamics.

INSHORE FAUNA (depth < 20 m)

The sediment at station 93 at a depth of 18 m has a high sand (68 percent) content as opposed to an average of seven percent at 70 m depth, while the other sites averaged less than two percent sand. The organic content (loss on ignition) of the sediment varied from one percent at station 93 (18 m) to nine percent at station 81 and 41. The major component of the fauna at the Niagara

station 93 at a depth of 18 m are the Sphaeriidae, with Sphaerium nitidium and S. corneum predominant (Table 20). Oligochaetes are next in importance, with the species Limnodrilus hoffmeister, Quistadrilus (Peloscolex) multisetosus, Tubifex tubifex and Ilyodrilus templetoni present. At the stations sampled, the chironomids were most numerous at this shallow station (93 - 18 m), although they represented only 0.3 percent of the total biomass. The species present, in descending order of abundance were: Heterotrissocladius changi, Paracladopelma sp., and Procladius spp., with a few Micropsectra sp., Chironomus salinarius grp. and Monodiamesia bathyphila present. The chironomid distribution and species composition is richest in the shallow nearshore zone of Lake Ontario (Golini, 1979).

OFFSHORE FAUNA (depth > 30 m)

As in all the Great Lakes except Lake Erie, the benthic fauna inhabiting the hypolimnion of Lake Ontario is dominated by Pontoporeia, which comprised between 87 and 90 percent of the total biomass present at the sites sampled (Tables 21 to 23). The population dynamics and statistics of this dominant amphipod are discussed separately. Oligochaetes are next in importance with Stylodrilus heringianus and Tubifex tubifex being the dominant species. Pisidium spp. and the chironomid, Heterotrissocladius oliveri are minor components of the deep-water fauna, each comprising less than one percent of the total biomass (Fig. 19).

Analysis of variance of the populations indicated considerable temporal variation at each sample station. The variations of total oligochaetes and sphaeriid clams between 1981 and 1983 were significant ($p<0.05$, df 8,26) at

TABLE 20: Abundance of major fauna, shell free dry biomass ($mg.m^{-2}$), and percent composition of total biomass at station 93 from 18 m depth during 1983 (April, July, and November). Standard error (SE) in brackets.

Stn. 93(18m) Organism	Average	(SE)	Biomass	(SE)	% Biomass
Total fauna	6714.0	(1136.5)	5589.9	(1761.5)	
Pontoporeia	2381.0	(607.7)	820.6	(123.5)	14.6
Gammarus	25.7	(11.3)	11.6	(5.9)	0.2
Asellus	73.6	(8.9)	38.1	(10.6)	0.7
Oligochaetes	2723.7	(488.0)	1016.0	(401.7)	18.1
Pisidium spp.	117.0	(60.6)	10.9	(5.6)	0.2
Sphaerium spp.	1201.3	(509.4)	3623.0	(2186.9)	64.4
Gastropoda	6.3	(1.4)	28.1	(25.0)	0.5
Total chironomids	158.6		15.9 mg		0.28
Tanypodinae	19.0	(11.5)	2.5	(1.4)	0.04
Orthocladiinae	105.3	(91.0)	8.5	(7.2)	0.15
Tanytarsini	1.3	(1.3)	0.1	(0.1)	0.0
Chironomini	33.0	(21.3)	4.8	(1.7)	0.08

TABLE 21: Abundance, dry biomass ($mg.m^{-2}$), and percent composition at station 81 from 35 m depth during April, July, and November, 1981 to 1983. Standard error (SE) in brackets.

Stn. 81(35m) Organism	Average	(SE)	Biomass	(SE)	% Biomass
Total fauna	7500.0	(965.5)	2615.6	(243.9)	
Pontoporeia	6531.0	(988.5)	2344.2	(230.3)	89.6
Asellus	17.8	(13.4)	7.1	(4.3)	0.03
Oligochaetes Stylodrilus	1.7	(0.4)	5.9	(0.1)	0.2
Tubificids	642.6	(131.8)	215.6	(33.4)	8.2
Chironomids Procladius	1.0	(1.0)	0.1	(0.3)	0.0
Orthocladiinae	4.5	(3.6)	0.4	(0.3)	0.0
Chironomus	4.2	(4.2)	0.3	(0.3)	0.0
Pisidium	223.3	(58.3)	21.7	(5.8)	0.8
Sphaerium	0.4	(0.4)	7.0	(7.0)	0.2
Mysis	4.4	(2.2)	4.1	(2.2)	0.1
Ostracods	24.3	(13.7)	0.6	(0.3)	0.0
Turbellaria	7.5	(5.9)	7.2	(5.6)	0.2

TABLE 22: Abundance, dry biomass ($mg.m^{-2}$), and percent composition at Station 93 from 70 m depth during April, July, and November, 1981 to 1983. Standard error (SE) in brackets.

Stn. 93(70m) Organism	Average (SE)		Biomass (SE)		% Biomass
Total fauna	5508.7	(1992.3)	2554.8	(286.7)	
Pontoporeia	4556.6	(1733.1)	2250.8	(801.2)	88.06
Gammarus	6.4	(5.3)	4.6	(3.7)	0.2
Asellus	8.2	(18.3)	5.4	(12.2)	0.2
Oligochaetes					
Stylodrilus	261.2	(59.0)	92.5	(30.9)	3.6
Tubificids	338.0	(61.7)	126.3	(25.5)	4.9
Chironomids					
Tanypods	1.9	(5.3)	0.5	(1.3)	0.02
Orthoclads	24.8	(40.1)	14.1	(34.8)	0.5
Sphaerium	1.0	(2.8)	15.8	(44.6)	0.6
Pisidium	300.7	(213.5)	22.7	(19.8)	0.9
Gastropods	3.8	(3.3)	4.8	(4.1)	0.18
Mysis	16.9	(16.2)	16.7	(16.2)	0.6
Candona	0.6	(1.7)	0.1	(0.1)	0.0
Helobdella	3.8	(3.4)	3.2	(2.9)	0.12

TABLE 23: Abundance, dry biomass ($mg.m^{-2}$), and percent composition at Station 41 from 125 m depth during April, July, and November, 1981 to 1983. Standard error (SE) in brackets.

Stn. 41 (125 m)

Organism	Average	(SE)	Biomass	(SE)	% Biomass
Total fauna	2332.4	(271.4)	830.4	(76.6)	
Pontoporeia	1968.5	(221.5)	724.4	(58.3)	87.2
Oligochaetes					
Stylodrilus	350.2	(48.2)	90.7	(13.7)	11.0
Tubificids	11.1	(4.3)	2.9	(1.1)	0.3
Chironomids					
Heterotrissocladius	7.2	(6.7)	0.8	(0.7)	0.1
Pisidium	30.4	(6.9)	2.0	(0.5)	0.2
Mysis	28.9	(8.3)	30.2	(8.6)	3.6
Candona	2.0	(1.5)	0.1	(0.1)	0.0
Calanoid	7.1	(3.1)	0.1	(0.1)	0.0

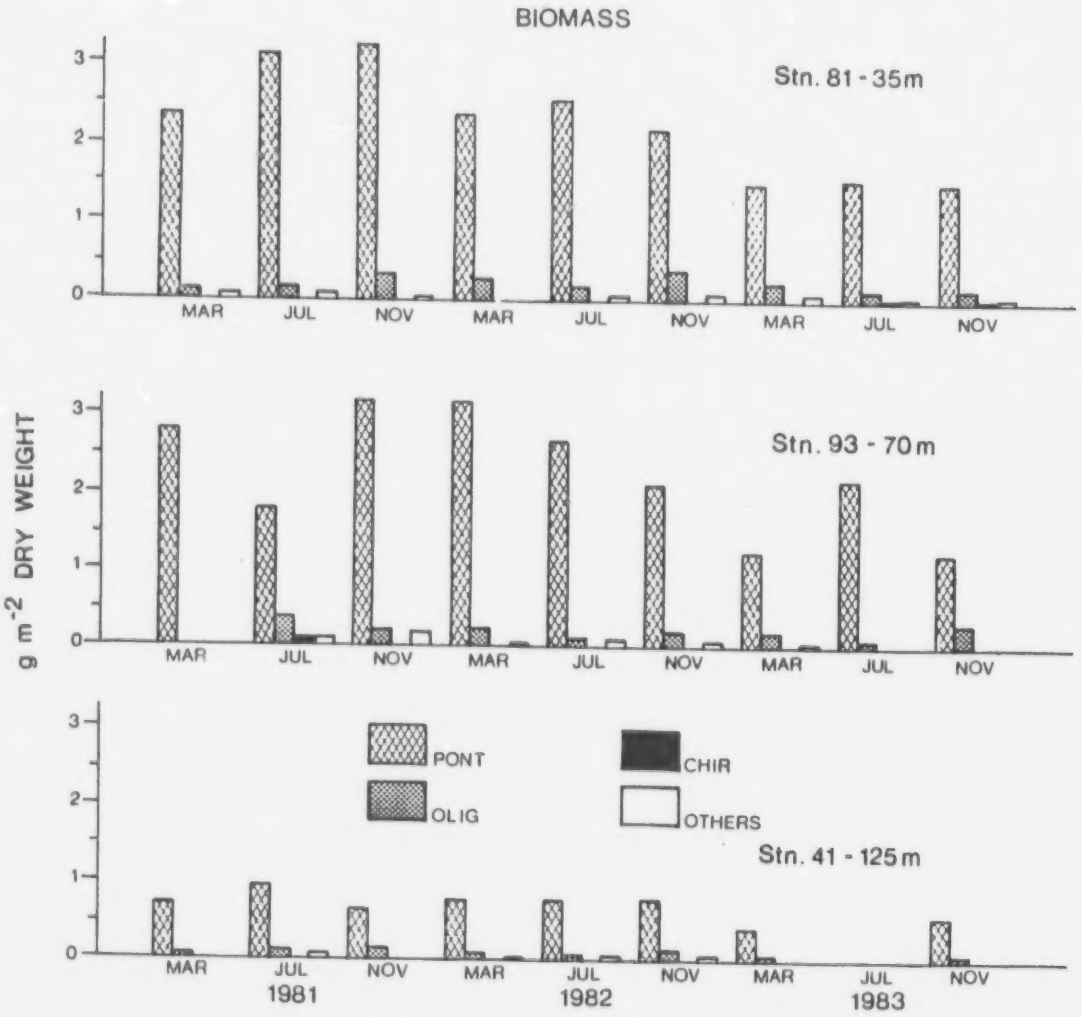

Figure 19. Biomass of benthic fauna (g m^{-2} dry weight) at three depths in Lake Ontario, sampled April, July and November, 1981 to 1983.

both stations 81 and 93A (70 m). Populations of both oligochaetes and Sphaeriidae were highest during late fall and lowest during mid-summer, reflecting the breeding cycles of these organisms (Figs. 20 and 21). A proportion of the high variability between years is due to error in sample analysis. Samples were collected, sorted or analyzed by different persons each year, resulting in changes of efficiency.

As a result of the variance among sample dates, there were no significant differences between the populations of total oligochaetes or Sphaeriidae present at stations 81 and 93A (70 m). When using only the monthly 1982 data there was a difference between the number of sphaeriids at station 81 and 93A (70 m), ($p<0.01$, df 1,16). Species differences between stations existed, reflecting the depth differences of the stations. The population size of Stylodrilus was significantly less ($p<0.01$, df 1,16) at shallower station 81 (35 m, Kingston basin) than at the deeper station 93A (70 m) off the mouth of the Niagara River.

The population of invertebrates was significantly lower at the deeper mid-lake station (41 at 125 m) than at the two inshore stations sampled (81 at 35 m and 93 at 70 m). The populations of Pontoporeia, total oligochaetes, as well as the sphaeriid clams (Pisidium conventus) were all significantly lower at station 41 than at the two more inshore stations ($p<0.01$, df=2,25). During 1983, the total invertebrate population at station 12 (105 m) and station 41 (125 m) averaged 2030 and 1636 per m^{-2} respectively. However, there were no significant differences between the numbers of Pontoporeia or oligochaetes at these two stations (Tables 23 and 24). The average invertebrate fauna at station 41 between 1981 to 1983 was much lower (2332 m^{-2}) than at the other sites sampled (Tables 21 - 24).

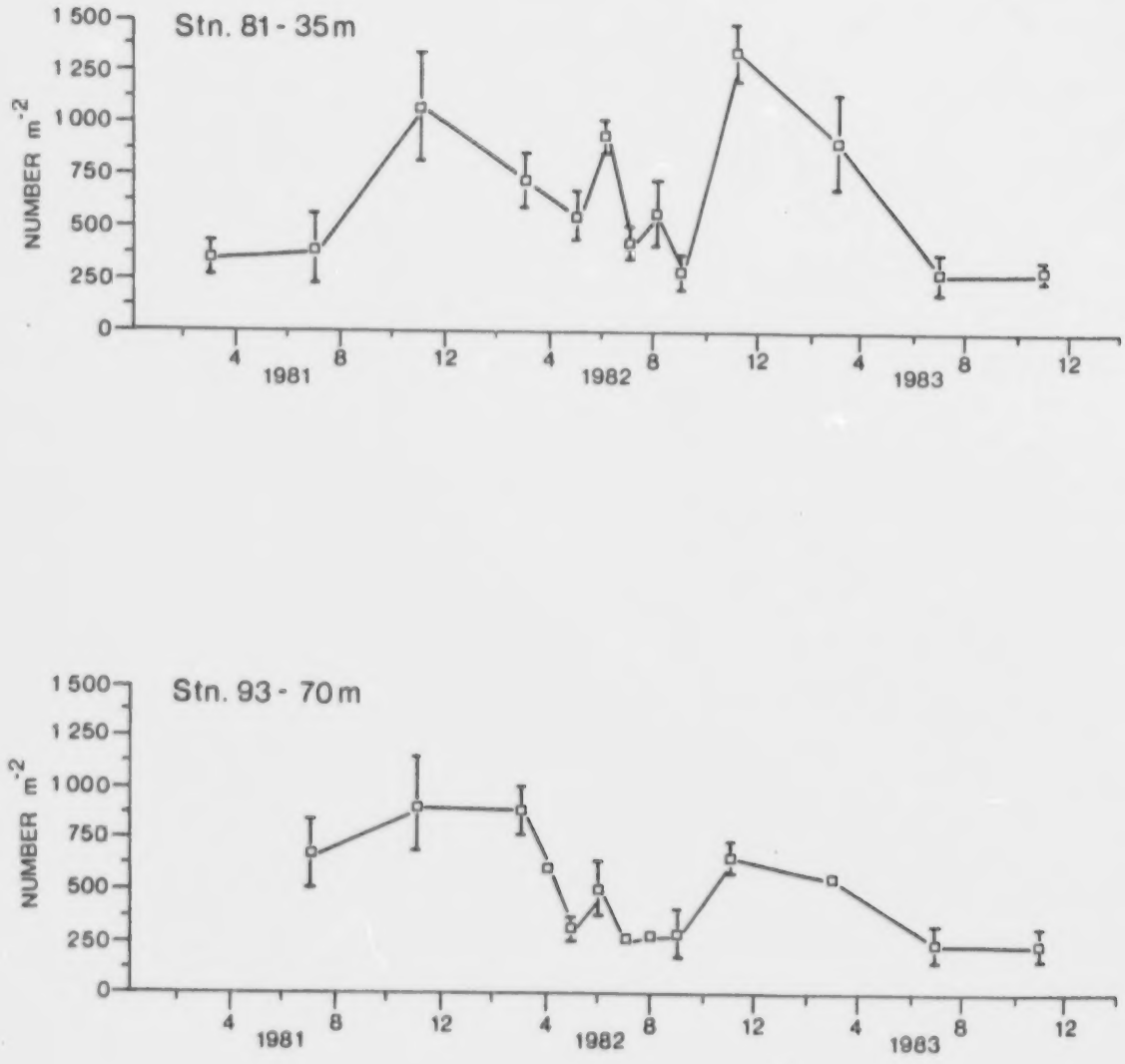

Figure 20. Seasonal trends in total oligochaetes populations in Lake Ontario at stations 81 and 93A, 1981 to 1983. Samples examined monthly during 1982, three times during the other years. Interval bars represent 95 percent confidence intervals.

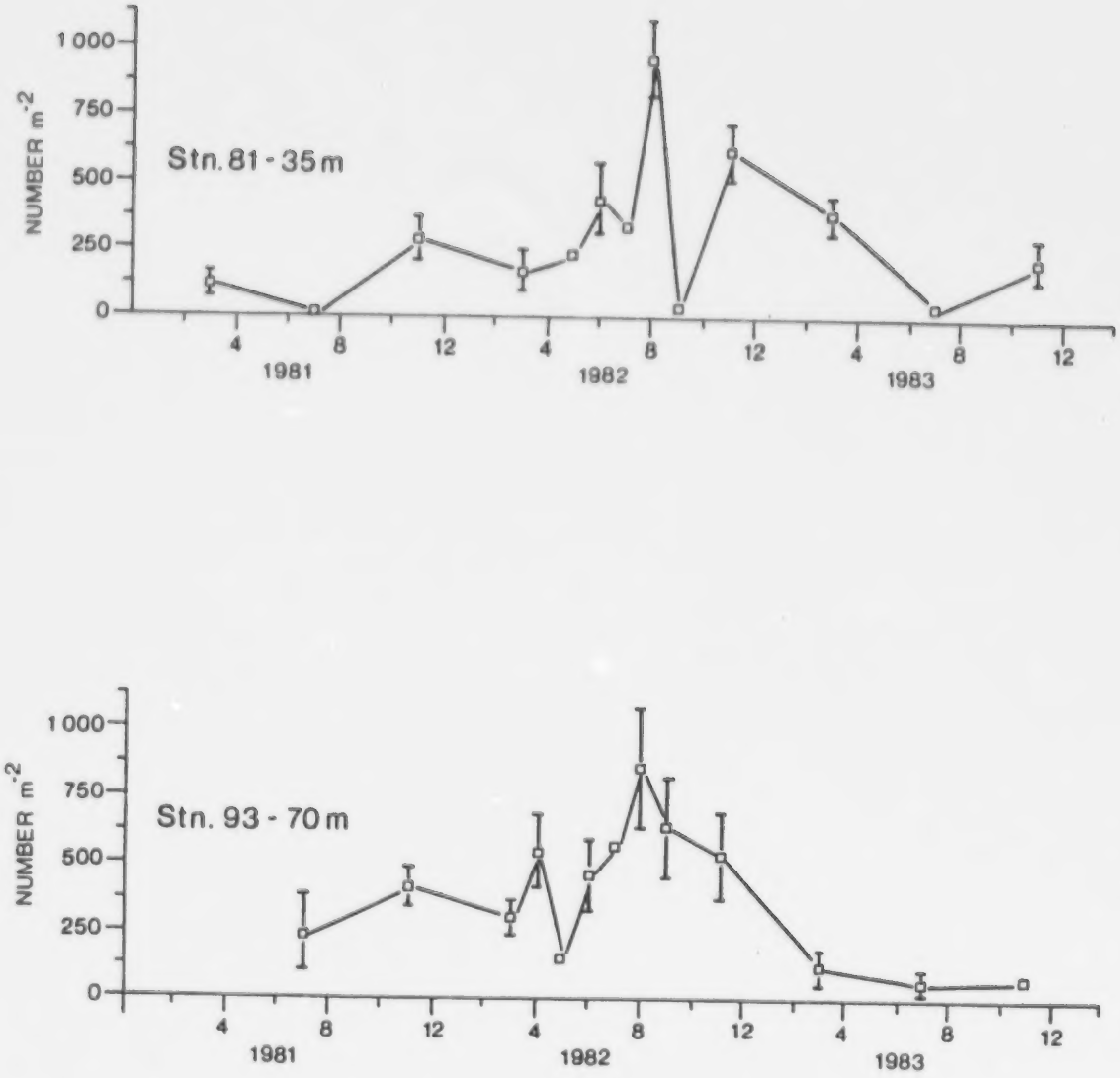

Figure 21. Seasonal trends in Sphaeriidae populations in Lake Ontario at stations 81 and 93A, 1981 to 1983.

TABLE 24: Abundance, dry biomass ($mg.m^{-2}$), and percent composition at Station 12 from 105 m depth, April, July, and November, 1983. Standard error (SE) in brackets.

Stn 12 (105 m)

Organism	Average	(SE)	Biomass	(SE)	% Biomass
Total fauna	2031.4	(381.3)	585.8	(238.1)	
Pontoporeia	1415.6	(293.4)	447.3	(180.8)	76.3
Oligochaetes Stylodrilus	476.8	(85.0)	101.9	(49.6)	17.4
Tubificids	32.3	(5.7)	12.7	(6.2)	2.2
Chironomids Heterotrissocladius	30.9	(9.9)	2.3	(0.9)	0.4
Micropsectra	3.4	(0.1)	1.0	(0.0)	0.0
Pisidium	32.1	(12.9)	5.8	(3.0)	1.0
Mysis	17.0	(0.3)	13.6	(0.3)	2.3
Candona	6.0	(3.2)	0.2	(0.1)	0.0
Calanoid	7.1	(3.1)	0.1	(0.1)	0.0

PONTOPOREIA

There were no significant temporal differences in numbers of Pontoporeia at stations 81 or 41 (df 13,65). At the Niagara station (stn 93A at 70 m) there was an increase in population over the winter of 1981 to 1982 ($p<0.05$, df 7, 35). There was no spatial difference in population of Pontoporeia at station 81 at 35 m (Kingston) versus station 93A at 70 m (Niagara)(Tables 21 and 22). However, there were significantly fewer animals ($p<0.01$, df 2,21) at the deeper station 41 in the middle of the lake (Fig. 22).

There was no difference in the growth rates of the young of the year Pontoporeia at stations 81 (35 m depth) and 93A (70 m) during either 1981 or 1982 (Fig. 23). Covariance analysis indicated no difference in the growth rate regressions of the young Pontoporeia during 1981 versus 1982. The occurrence of two reproductive periods at the deep station 41 prevented the calculation of cohort growth rate at that site.

The respiration rates of the amphipods from the three stations were similar at 5°C. At 7°C the respiration rate of the Niagara population was slightly higher than those at the other two stations. Expectedly, the respiration of the deep water population of station 41 at 10°C was higher than those at the other stations, as the deep water populations never experience temperatures much above 6°C. The calculated regression between respiration (R), temperature (T) and size was:

$$R\ (mg\ O_2\ mg^{-1} hr^{-1}) = Exp\ (-7.19 + .036T - 0.219\ Ln\ weight\ [mg\ dry]).$$

$$r^2 = 0.6$$

The calculated size frequency production of Pontoporeia at the three stations ranged from a low of 1.71 g m^{-2} (dry weight) at station 41 to a

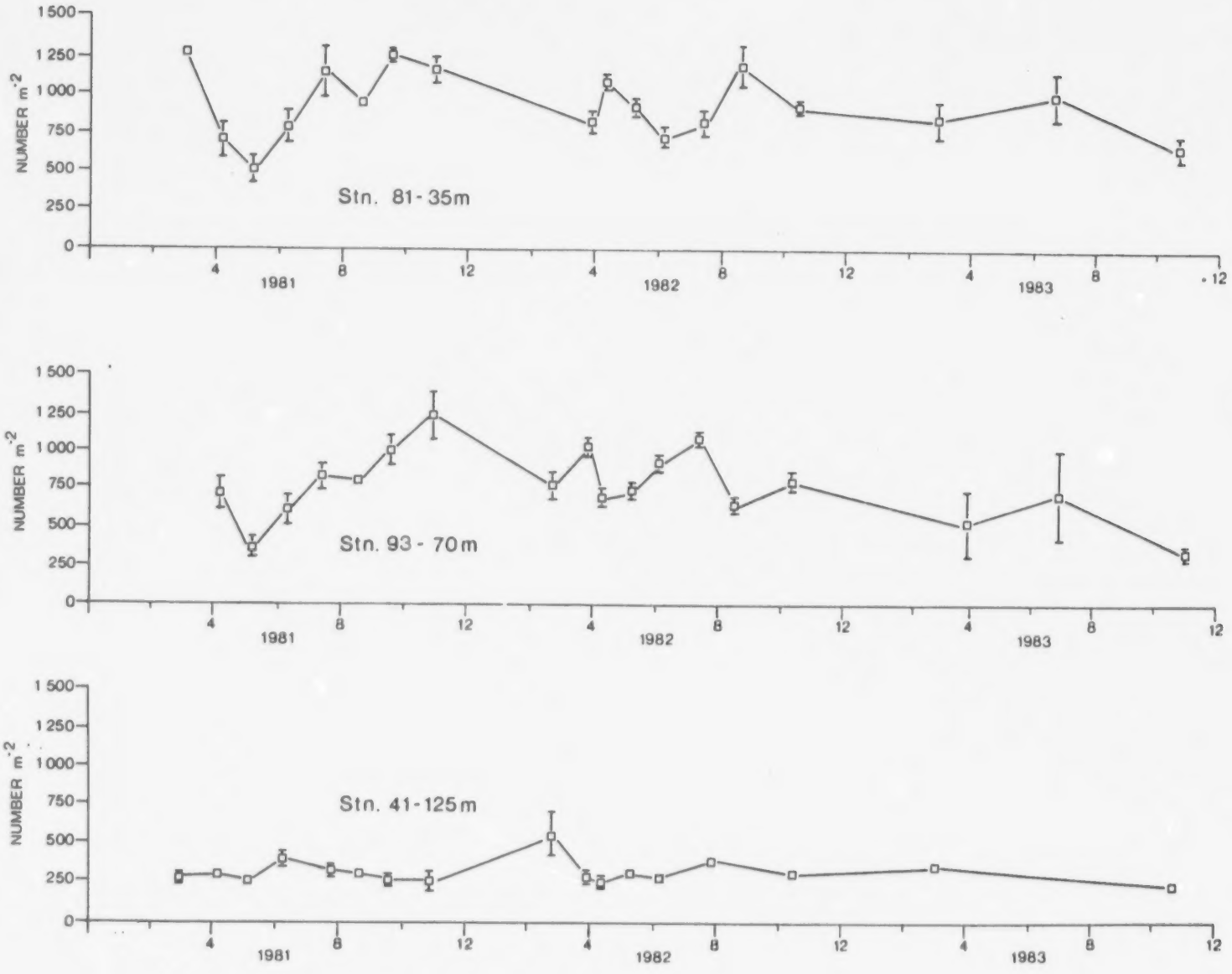

Figure 22. Seasonal trends in Pontoporeia populations at three stations in Lake Ontario between March 1981 and November 1983. Interval bars are 95 percent confidence limits.

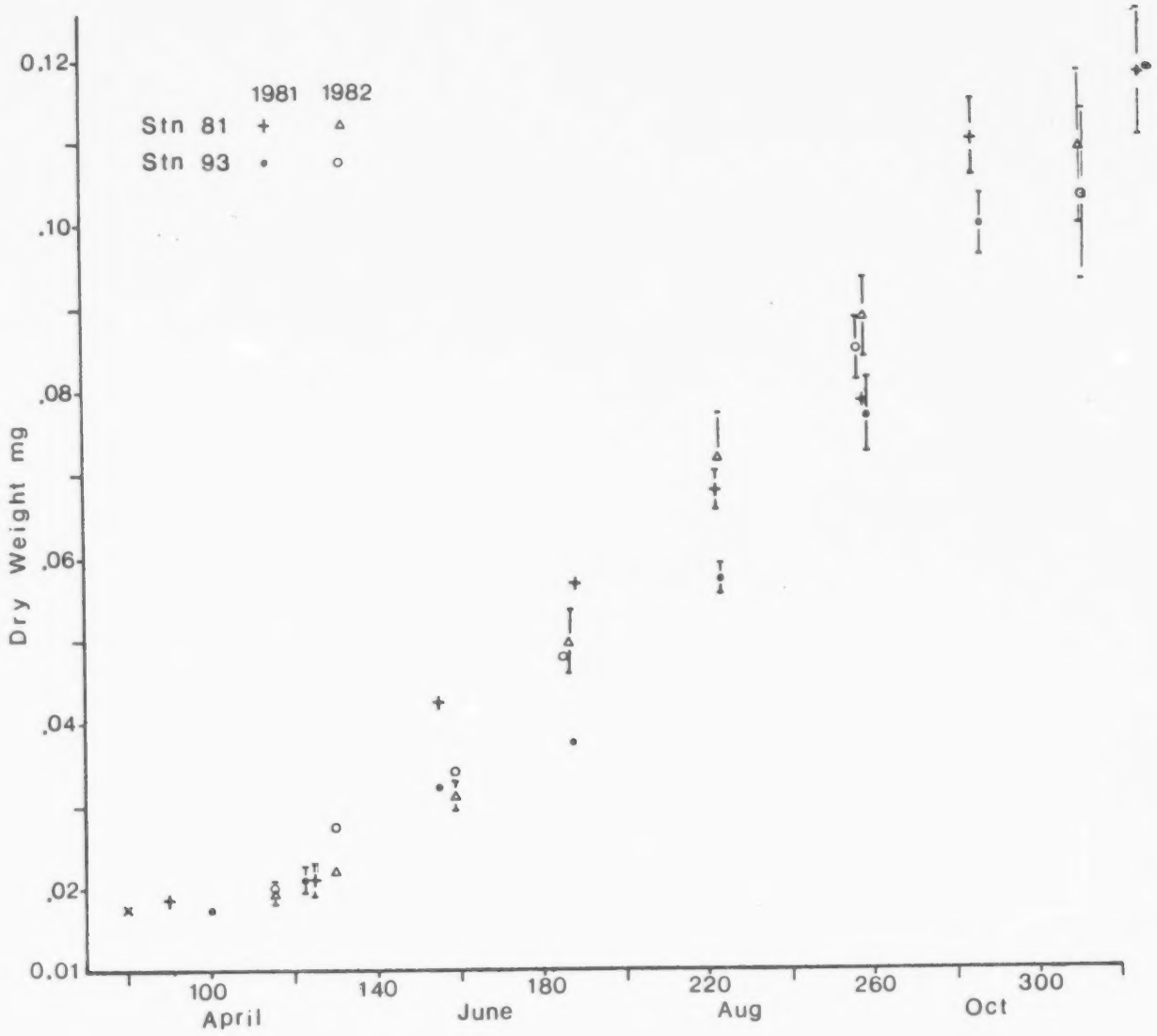

Figure 23. Growth rates of young of the year Pontoporeia at stations 81 and 93A during 1981 and 1982. Weight of eggs (x) prior to hatching in April averaged 0.0174 mg.

high of 5.48 g m^{-2} at station 81. However, there were no significant differences between years or stations 81 and 93A (Table 25). Exponential production based on the three cohorts at each station was lower than that calculated by size frequency. However, the dual cohorts present at station 41 makes the exponential production estimate unprecise.

DISCUSSION

The skewed composition of the deep water fauna with its predominance of Pontoporeia has occurred since the 1960s (Hiltunen, 1969) and is normal in most deep, glacial lakes. Golini (1979) found fewer than 100 molluscs and chironomids present per m^2 in the deeper offshore areas of Lake Ontario, while the lumbriculid worm Stylodrilus, and amphipod Pontoporeia were most abundant at depths less than 100 m. Golini related the richer benthic fauna in the shallow zone around Lake Ontario to the larger food source within the nearshore belt, and the shorter settling distance of the phytoplankton to the bottom of the inshore area. A further influence on population size, is the river effect of the major clockwise currents, which distributes material from the tributary estuaries along the shore.

Stylodrilus has been used as an oligotrophic-indicator species (Hiltunen, 1969) and is common in the deeper areas of the Great Lakes (Howmiller, 1974). This oligochaete is displaced by tubificids in fine sediments at intermediate depths and in more enriched areas. However, Stylodrilus is usually common in well oxygenated environments, ranging from cool streams, shallow sandy sediments, or deep cold water. In the offshore region of Lake Ontario,

TABLE 25: Mean annual production (dry weight) and 95% confidence intervals of Pontoporeia at three sites in Lake Ontario calculated by size frequency method. Numbers corrected for number of young hatched; in brackets the uncorrected averages collected between July and November.

	STN 81	STN 93A	STN 41
DEPTH (M)	35	70	125
1981 No.m^{-2}	7182 ± 1798 (5481 ± 776)	4985 ± 798 (4825 ± 1089)	3128 ± 0906 (1753 ± 271)
BIOMASS g.m^{-2}	3.05 ± .26	2.24 ± 0.43	0.99 ± 0.18
PROD. g.m^{-2}	5.49 ± 5.16	5.15 ± 6.72	2.00 ± 1.43
T.R. (P/B)	1.79	2.3	2.01
P.Exp g.m^{-2}	2.74	1.31	0.71
1982 No.m^{-2}	8653 ± 2655 (4834 ± 1116)	6726 ± 1931 (4652 ± 976)	3205 ± 0408 (1800 ± 342)
BIOMASS g.m^{-2}	2.59 ± .20	2.42 ± .21	0.75 ± 0.13
PROD. g.m^{-2}	4.81 ± 3.29	4.18 ± 2.81	1.72 ± 2.22
T.R. (P/B)	1.86	2.04	2.29
P.Exp g.m^{-2}	3.38	2.13	0.55

P.Exp = exponential production

Stylodrilus has remained the dominant oligochaete since the 1960s (Brinkhurst et al., 1968)

The dominant invertebrates of Lake Ontario are the semi-benthic shrimp Mysis and the burrowing amphipod Pontoporeia. The latter species accounts for greater than 60 percent of the total benthic biomass in Lake Ontario. Pontoporeia, being a burrower, is not as readily available to the pelagic fish community as is Mysis, but both are very important to fish that are too small to consume other fish. The oligochaete Stylodrilus and the small Pisidium clams remain completely burrowed throughout their lifespan and are only available to bottom feeding fish. Pontoporeia often contain high lipid levels which, together with their abundance, makes the species important in the energetics of the lake, as well as the transfer of organic contaminants from the sediments in which they burrow to the fish community. An understanding of the biology, growth rate, and reproduction of the species are necessary in order to relate the contaminant levels in the amphipod to the cycling of contaminants in the lake.

Being a cold water species, the generation time of Pontoporeia is two years, after which the reproducing adults die. Reproduction normally occurs during late winter, so spring populations contain three cohorts; young-of-the-year (YOY), juveniles from the previous year, and gravid females which use up their lipid reserves during egg development. The YOY cohort can readily be followed throughout summer until they reach about 4 mm in length in late winter.

Until recently only one species (P. hoyi) was considered in the Great Lakes. However, E. L. Bousfield (pers. comm.) concurs that the deep water varieties brevicornis and filicornis may be separate species. These

deep-water populations often reproduce out of phase, and below 100 meters gravid females occur during both spring and late summer.

In spite of differences in phytoplankton abundance and the depth differences (35 m) between stations 81 and 93A, biomass and production by Pontoporeia were equal at the western and eastern ends of Lake Ontario. This is due to the influence of the Niagara River Plume as far out as 70 m depth. Debris from the river increases the amount of organic material available to the benthic populations along the south shore of the lake. This influence was also observed in the organic deposition zone and displacement of populations of Gammarus fasciatus and Physa lakeward to a depth of 40 m east of the Niagara River mouth. Kinney (1972) found a similar reduction in the usually dominant Pontoporeia and Stylodrilus populations at 35 m depth off the Niagara River, and replacement by a community representative of intermediate depths and harbours.

The fluctuations in the abundance of Pontoporeia were not significant at the sampled sites, although the biomass of the amphipod population dropped from 1981 until 1983. Part of the annual fluctuations in the standing stock may be due to varying phytoplankton production during 1981 to 1982. Cederwall (1976) found a similar annual fluctuation in abundance of the two species of Pontoporeia present in the Baltic Sea as a result of increased phytoplankton production. The two-year generation time of the species would dampen the response to fluctuations in algae production, with long term changes being required before a corresponding change in population size would occur. The major predator on Pontoporeia in Lake Ontario is the benthic sculpin, Cottus cognatus. However, as sculpin populations remained similar during 1980 to

1983 (O'Gorman et al., 1984), predation should have been similar between 1981 to 1983. The extent to which fish and Mysis predation (Parker, 1980) controls the annual fluctuations of Pontoporeia in Lake Ontario is only speculative. Ankar (1977) found that fish predation was a minor fraction of the total benthic production in the Baltic. However, he concluded that even in the well studied Baltic, not enough was known about the biology of the dominant macrobenthos to understand the energy balance and controlling factors of the benthic community.

In comparison to 1964 (Hiltunen, 1969) and 1971 (Nalepa and Thomas, 1976) the Pontoporeia populations in the shallow (10 to 40 m) and deep zones (>100 m) were significantly less than those at the single stations during 1981 and 1982 ($p<0.05$ df 1,29, and $p<0.01$ df 1,26 resp.). Golini (1979) found a similar reduction of benthic populations in the deeper waters of the lake. There were no differences between the populations of the intermediate zone (40 to 100 m) during 1964, 1972, and 1977 and the single site at station 93A during 1981 or 1982.

The total biomass (standing stock) and production of Lake Ontario were calculated for the depth zones (Table 26). The ratios between the average populations of Pontoporeia in the shallow (20 to 40 m), intermediate (40 to 100) depth zones during 1964 to 1977 (Hiltunen, 1969; Nalepa and Thomas, 1976; Golini, 1979) and that at the single sites 81 (35 m) and 93A (70 m) were used to estimate the lake-wide populations in Lake Ontario during 1981 and 1982. For the marginal depths of 10 to 20 m and 150 to 240 m, which were not sampled, the average ratio of numbers with that in the closest depth zone were used to estimate population sizes during 1981 and 1982 (Table 26). The

TABLE 26: Calculated Pontoporeia production (dry weight) in Lake Ontario. Average number (April-November) and biomass (B) includes number of eggs produced. Ba and Pa are the total biomass and production calculated for each depth zone.

Depth Zones		1981			1982	
10 - 20 m	n =	1327	m^{-2}	n =	1600	m^{-2}
Area = 1.44 E9 m^2	B =	0.56	$g.m^{-2}$	B =	0.48	$g.m^{-2}$
(as 0.44 x No. at	Ba =	0.81	E6 kg	Ba =	0.69	E6 kg
20 -40 m)	Pa =	1.45	E6 kg	Pa =	1.27	E6 kg
21 - 40 m	n =	3016		n =	3634	
Area = 2.57 E9 m^2	B =	1.28		B =	1.09	
(as 0.42 x No. at	Ba =	3.29		Ba =	2.80	
Stn. 81)	Pa =	5.90		Pa =	5.18	
41 - 100 m	n =	2642		n =	3564	
Area = 5.30 E9 m^2	B =	1.18		B =	1.28	
(as 0.53 x No. at	Ba =	6.29		Ba =	6.78	
Stn 93)	Pa =	14.46		Pa =	13.82	
101 - 150 m	n =	3128		n =	3205	
Area = 4.39 E9 m^2	B =	0.99		B =	0.75	
(as No. at	Ba =	4.35		Ba =	3.29	
Stn. 41)	Pa =	8.78		Pa =	7.53	
151 - 237 m	n =	1532		n =	1570	
Area = 3.80 E9 m^2	B =	0.49		B =	0.37	
(as 0.49 x No. at	Ba =	1.84		Ba =	1.39	
Stn. 41)	Pa =	3.72		Pa =	3.19	
	Σ Ba =	16.59 E6 kg		Σ Ba =	14.96 E6 kg	
	Σ Pa =	34.34 E6 kg		Σ Pa =	30.99 E6 kg	

calculated mean dry weight per individual and turnover ratios (T.R.) at the three stations were averaged for 1981 and 1982. The average T.R. during 1981 to 1982 was nearly identical to that calculated for Pontoporeia in eastern Lake Ontario during 1968 (Johnson and Brinkhurst, 1971). These averages were then used with the estimated populations in the depth zones to calculate the lake-wide biomass and production of Pontoporeia during 1964, 1972, and 1977. Shipex and Smith-McIntyre grab sample counts were converted to Ponar equivalents using Powers and Robertson's (1967) and Flannagen's (1979) sampling efficiencies. The estimated production for the whole lake ranged from 21.7 K metric Tonnes (dry weight) in 1972 to 34.1 K Tonnes in 1981 (Table 27). In comparison, maximum fish catch in Lake Ontario during 1915 to 1925 (Christie, 1974) was 2.6 K Tonnes (wet).

The estimated production of Pontoporeia was greater during 1968 at both the eastern basin and in the deep central region of Lake Ontario (in Johnson and Brinkhurst, 1971: Lake Ontario site [28 m] and Federal Water Pollution Control Administration site [100 m]). This decrease in production may reflect the reduced phytoplankton abundance in the lake. Exact site comparisons with other surveys are difficult due to the heterogeneity of the bottom fauna and changes in production due to temperature and depth differences of sites (Seigfried, 1985).

TABLE 27: Calculated total standing stock biomass and 95% confidence interval during September (as 10^3 Tonnes dry weight), and total annual production of Pontoporeia in Lake Ontario, below the 10 m contour.

Year	1964*	1972	1977	1981	1982
Number of Sites	24	55	153	3	3
Biomass 10^3 T.	18.29 ±13.42	10.61 ±4.35	15.95 ±13.70	16.59	14.96
Production 10^3 T.	37.80 ±27.70	21.70 ±8.76	32.56 ±28.00	34.34	30.99

Lake Area below 10 m contour = 1.75 E 10 m^2

* based on 3 depth zones (<40; 41 to 100; >101 m)

PROGRAM ASSESSMENT

The Bioindex Program is well designed for general long-term subvertebrate community monitoring. Changes in the functioning of the biological community manifest themselves as changes in community abundance and/or structure at some point during the season. Therefore, analyses of samples at the more detailed level of species composition are much more informative of the state of the system than general biological variables such as POC, PON, and CHLA.

Community structure can be treated analytically as a whole, using similarity/dissimilarity indices, or it can be broken into its component parts, species (indicator species, population growth patterns) and biomass, which provide additional information. To gain the most information it is best to analyze the data at all three levels. Methods for analyzing trends in community structure are now being developed. Johannsson and Minns (manuscript in prep.) have formulated a composite dissimilarity index for communities that vary along a continuum, such as pelagic phytoplankton and zooplankton communities, and have successfully used this index to compare the 1981 to 1983 Bioindex phytoplankton communities across years and among stations. Indices are particularly appropriate for monitoring because they reduce community comparisons to a single meaningful number which can be used in multivariate and trend analyses.

Biological monitoring must include all major biological components of the ecosystem because different components are more susceptible to different environmental stresses. The phytoplankton are most responsive to changes in lake trophy, while the zooplankton are more directly affected by invertebrate

and vertebrate predators. Benthic invertebrates are a key in the food web, linking phytoplankton and detritus to fish. They are also exposed to the high sediment contaminant levels in the depositional basins. Fish respond directly to changes in the physical habitat, competition, food supply and predation (including fishing pressure). In addition, as a top predator, fish are the most susceptible of the aquatic forms to accumulation of lipophilic toxic chemicals. Since the physical and chemical environment affect the growth of all biological components, these parameters must also be measured routinely to interpret changes in the biological community.

The Bioindex Program does not include a fisheries component, although other agencies, such as the Ontario Ministry of Natural Resources and the U.S. Fish and Wildlife Service, conduct regular surveys to measure the abundance of some Lake Ontario fish stocks. On the other hand, the Bioindex Program is the only program to regularly sample the open-water pelagic and benthic communities. As such, it provides a valuable input to an integrative Lake Ontario biological monitoring program.

The strategy of the Bioindex Program of sampling one or a few stations frequently, has been questioned for a water body as large as Lake Ontario. Horizontal water movements in the lake are significant (Boyce, 1974; Simons, 1976). Due to continuous inputs, differences in inshore-offshore seasonal thermal developments and current patterns, the lake is not homogeneously mixed in the horizontal plane. Water masses in different regions of the lake may differ in the state of development of the seasonal cycle, nutrient concentrations and thermal structure. The surface waters in the nearshore areas are subject to the Coriolis' force and wind-driven horizontal

circulation with horizontal particle velocities of approximately 10 $cm.s^{-1}$ or 60 $km.wk^{-1}$ (Boyce, 1974). The middle of the lake is subject to the slower forces of surface wind drift and wind-driven surface gravitational waves which move particles at approximately 1 to 2 $cm.s^{-1}$ or 8 to 16 $km.wk^{-1}$ (Boyce, 1974). When sampling one location repeatedly the seasonal patterns observed in all parameters could be affected by the passage of different water masses. Analysis of changes in cladoceran population sizes with cumulative epilimnetic temperature produce more coherent patterns when the data are separated on the basis of epilimnetic chloride concentration (Fig. 24). Chloride is a conservative measure and changes in the chloride levels signal the passage of water bodies with different histories. However, analysis of temporally adjacent (one week apart) phytoplankton communities, using "Percent Dissimilarity," rarely detected significant changes in community structure coincident with changes in chloride concentration (Table 28). Nor were changes in algal biomass related to changes in chloride concentration (Table 28). Clearly, the spatial differences within the region of the lake which will pass by the sampling station are rapidly outweighed by the rate of seasonal changes in the phytoplankton community, but not the zooplankton community. This may be due to the more even dispersion of species and rapid growth rates of phytoplankton as compared with zooplankton and may be further influenced by differences in fish distributions. Therefore, although different water masses are sampled through the year, they are rarely important to the analysis of the phytoplankton data. Different water masses could however, affect the detailed interpretation of the zooplankton data.

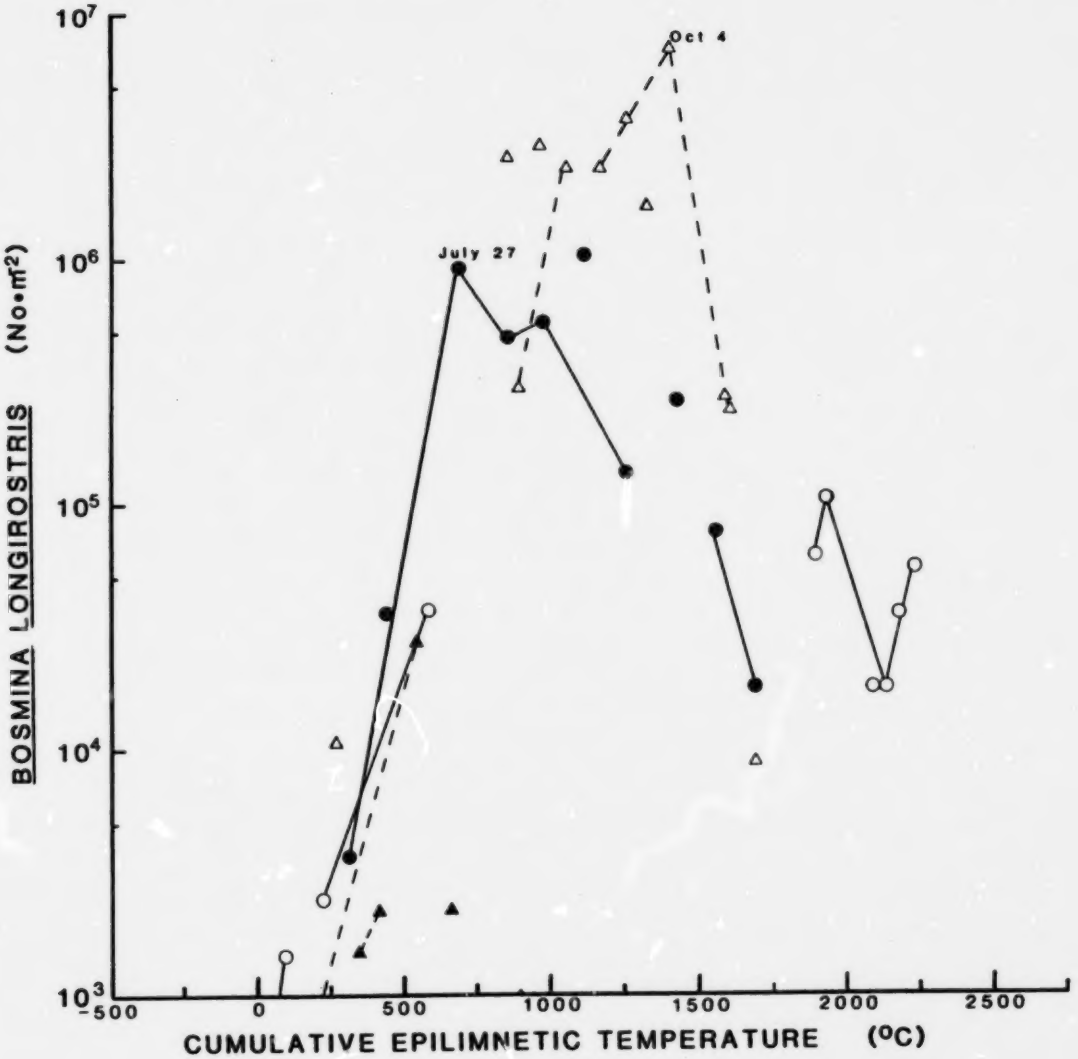

Figure 24. Bosmina longirostris population dynamics revealed by joining only those observations made under similar chloride conditions. Open symbol (water temperature < 14 C), solid symbols (water temperature > 14 C). 1981 (▲), 1982 (△).

TABLE 28: The correlation between changes in (a) phytoplankton community structure (1982) calculated in terms of both biomass and abundance and (b) total phytoplankton biomass (1981 and 1982), and changes in chloride concentration between adjacent weeks.

Station	Community Structure			Total Biomass	
	Biomass-r	Abundance-r	(N)	r	(N)
12	0.261	-0.218	(21)	-0.176	(51)
41	-0.140	-0.372	(24)	0.019	(52)
81	0.348	0.322	(23)	0.526	(51)
93	0.243	0.396	(28)	0.129	(55)
All	0.305	0.227	(96)	0.222	(209)

A few changes should be made in the sampling methodology of the Bioindex Program. All variables, except dissolved oxygen and vertical profiles of temperature and transparency, should be determined from integrated water samples so that the data are directly comparable. Zooplankton sampling must be extended into the hypolimnion and net efficiencies must be investigated. The weekly sampling interval should be maintained. It is frequent enough to follow phytoplankton community changes: any longer a time interval would greatly increase the variability of the biological and some nutrient parameters. A more extensive seasonal cross-calibration of the two major Lake Ontario phytoplankton data bases is recommended.

Annual samples are adequate to describe the benthic communities in Lake Ontario, due to the long generation times of the fauna (one to two years). Because of this, persistent long-term changes in the community will only appear gradually. At least five years of data are required in order to relate benthic population size to changes in phytoplankton abundance. However, in order to determine the reproductive success and growth during the summer, as well as mortality over the winter, spring and fall samples are needed. These data are important for interpreting the relationships with the fish community. Monthly sampling of benthic invertebrates are not necessary because an estimate of production as turnover time, is dependent primarily on mean temperature. Once established for a community, it varies little from year to year. Changes in food supply or predation pressure will be expressed through changes in abundance and/or biomass.

At least four replicate samples of benthos should be collected in order to account for the error in the sampling gear. Early spring (pre April 30th) and late fall (after October 1st) are the most suitable dates for collection. M. G. Johnson's eastern Lake Ontario benthic data (1968 to 1984) should be correlated with the nearby station 81, and incorporated into the Bioindex data base.

Station 93 should be dropped from the program. It is very shallow (17.5 m) and frequently disrupted by physical changes and perturbations. These increase the variability, decrease the continuity, and render interpretation difficult, especially of the biological variables.

The Bioindex Program is designed as a monitoring program. The information collected is sufficiently detailed to develop hypotheses concerning the functioning of the system, but it cannot test these hypotheses. The interpretability of trends, changes or specific community structures is dependent on the research data of other investigators. The historical trends observed in the phytoplankton and zooplankton community would be uninterpretable without previous work on indicator species, phosphorous-algal biomass relationships, and fish-zooplankton-phosphorous relationships. To an extent, the usefulness and success of the Bioindex Program will depend on our understanding of the Lake Ontario ecosystem.

As more becomes known about the Lake Ontario ecosystem the Bioindex Project may need to be modified. The roles of certain components of the pelagic food web need to be evaluated. These include the bacteria, ciliates, rotifers and mysids. In terms of research, work needs to be done on zooplankton-phytoplankton relationships, competition among zooplankton for

food, and on mysids - zooplankton interrelationships. This will answer the question as to what extent Mysis affects community structure and how dependent Mysis is on the epilimnetic zooplankton and phytoplankton for food. Further study is required on the relationships amongst fish species and Mysis, Pontoporeia, and zooplankton abundance; and on the paths of the water masses which pass the sampling stations, their variability, and controlling forces.

SUMMARY

With the acknowledgment that biological monitoring was fundamental to charting ecosystem health/state (Great Lakes Water Quality Agreement, 1978), the Bioindex, or Long Term Biological Monitoring Program was developed for Lake Ontario to: 1) determine normal seasonal patterns and ranges of abundance, community structure, and when possible, productivity of the biological components-phytoplankton, zooplankton, and benthos; 2) relate the biological components to variations in the physical, nutrient, and biological environment; and, 3) assess the adopted sampling strategy for long term monitoring.

As of 1981, in the epilimnetic or surface water (0 to 20 m), samples were collected weekly from March to November/December to measure physical, nutrient, and biological parameters at four stations, considered to be representative of the different open water environments in Lake Ontario (Fig. 1).

The present report examines the information from 1981 and 1982. The data were divided into five periods defined by temperature range and season. Seasonal, annual, and spatial variability were then examined using analysis of variance. Seasonal trends conformed with previously published data, except for chlorophyll a which showed no distinct seasonal pattern. There were significant differences in many variables between years and among stations. All general community measures (POC, PON, seston dry weight) and total algal biomass were higher at stations 12, 41, and 93 in 1981 than 1982, while zooplankton abundance was lower at all stations. Higher seasonal algal productivity at stations 12, 41,

and 93 in 1981 is suggested not only by the higher algal standing stock, but also by the higher seasonally weighted mean (SWM) temperatures, and lower SWM concentrations of SiO_2, NO_3NO_2, and TFP observed at these stations. The higher productivity was presumably due to the longer period of warm epilimnetic conditions in 1981. The changes in zooplankton abundance, on the other hand, are more likely related to the levels of fish predation.

The deeper mid-lake stations (12, 41) were more stable and less productive than the shallower nearshore stations (81, 93). Seasonally weighted mean levels of NO_3NO_2 were higher and temperature, TP, total algal biomass, and zooplankton abundance lower in the mid-lake than nearshore. In addition, the meso-eutrophic phytoplankton indicator species Melosira binderana, Stephanodiscus niagarae, and S. astrea var. minutula were "PRINCIPAL" species nearshore, and the meso-oligotrophic indicator species M. islandica and Synedra ulna, mid-lake.

Substitute measures of the biological (POC, PON, loss on ignition [LOI]) and phytoplankton (chlorophyll a [CHLA]) community did not correlate well with the direct biological measure, total algal biomass. The correlations were best in the spring, when all biological components of the pelagic community were increasing. Correlations were greater with CHLA than with POC, PON or LOI. In addition, the community parameters themselves measured different components of the ecosystem. Particulate organic carbon and PON did not correlate well with CHLA, nor with each other as the season progressed.

Multiple linear regression was used to identify the underlying relationships between the biological measures (POC, PON, CHLA, and total algal biomass) and environmental variables. This technique accounted for more of the variance in the data in the spring than at any other time, particularly in the mid-lake region. In the spring 72.1 percent of the variance in mid-lake total algal biomass was associated with the variation in TFP and EBT, and in the fall 60.5 percent with TFP, mixed depth, and effective light regime (ELR). Nearshore, in the spring, SRS (lagged one to three weeks) and ELR accounted for 42 to 46 percent of the variance, while in the fall EBT (-3), TFP (-3), and DZ/DM (-3) (euphotic:mixed depth), accounted for a non-significant percent to 76 percent of the variance. Chlorophyll a was related to SRS (0 to -3 lags) and NO3NO2 levels in all regions of the lake, with light an additional factor in the mid-lake region. In the spring 38 to 70 percent of the variance was explained depending on station location, and in the fall 39 to 45 percent. Particulate organic carbon behaved more like CHLA: variation in POC was best accounted for by changes in NO3NO2 (at all times), SRS (nearshore), light (mid-lake), and TFP (mid-lake). Particulate organic nitrogen was more closely related to total algal biomass. Temperature, TFP and ELR (-2) accounted for most of the variation in mid-lake PON levels, while SRS (-2 or -3) TFP and NO3NO2 best accounted for the PON values (nearshore).

These total algal biomass-environmental variable relationships are compatible with the models of Scavia (1979) and Simons (1976). The models also emphasize the need to incorporate additional loss factors, such as zooplankton grazing rates, into the analyses in order to account

for a greater percentage of the variation in algal biomass. More data, in the form of longer time series, are needed to perform similar analyses during the summer period.

Total algal biomass followed a repeated seasonal pattern of peaks and troughs in both years at the mid-lake stations. This resulted from a repeated pattern in basic species composition and seasonal changes in the dominant algal classes: Cryptophyceae, Bacillariophyceae, and Dinophyceae. Nearshore, the patterns were less stable although the same algal classes were dominant. In both regions the three classes contributed over 80 percent to the seasonally weighted mean algal biomass.

The same phytoplankton species were important mid-lake and nearshore, but they differed in their degree of importance and time of appearance. At all stations Cryptomonas erosa, Rhodomonas minuta, Gymnodinium helveticum, Peridinium aciculiferum, Dinobryon sertularia and Tabellaria fenestrata were "PRINCIPAL" species contributing over ten percent to sample biomass at least once at all stations in both years. At the mid-lake stations M. islandica and S. ulna were also "PRINCIPAL" species, and at the nearshore stations, M. binderana, S. niagarae, S. astrea var. minutula, Glenodinium spp., Ceratium hirudinella, Mougeotia spp., Oocystis spp. and Sphaerocystis schroeteri. All the "PRINCIPAL" species specific to one region of the lake were important, but less frequently abundant in the other region of the lake.

A comparison of seasonally weighted mean algal biomasses, and species compositions suggest that the trophic state of Lake Ontario may have decreased slightly between 1970 and 1981, 1982. Changes in the SWM algal biomasses from 2 to 4 $g.m^{-3}$ in 1970 to 1.2 to 1.8 $g.m^{-3}$

(corrected for contractor differences) in 1981, 1982 would indicate that the lake has progressed from meso-eutrophic to mesotrophic. Great Lakes indicator species, described by Stoermer and Yang (1969), Nicholls (1981), and Munawar and Munawar (1980), have changed from meso-oligotrophic:meso-eutrophic ratios of 0:6 and 2:7 in the earlier period to 3:4 in 1981, and 1982. Similarly, a comparison of the algal distributions in the Great Lakes in the early 1970s, based on the work of Munawar and Munawar (1981) and the early 1980s (present study), indicates that more species with oligotrophic distributions and fewer with eutrophic distributions are now common in Lake Ontario. Seven oligotrophic indicator species are now common as compared with zero to four in the early 1970s. This decrease in trophy corresponds with the period of decreases in phosphorous loading to Lake Ontario (Stevens and Neilson, 1986). These comparisons are suggestive of change, but not conclusive due to the small number of years available for comparison and to the variability between data bases associated with different contractors.

The zooplankton community structure has not changed significantly from 1967 to 1982. Cyclopoid copepodids and Bosmina longirostris are the predominant crustacean forms in the lake. Cyclops bicuspidatus thomasi and Trophocyclops prasinus mexicanus are the principal copepods, and B. longirostris, Daphnia retrocurva, Ceriodaphnia lacustris and Eubosmina coregoni the dominant cladocerans. Zooplankton abundance has changed dramatically between 1967 and 1982 with exceptionally low June to October abundances of $10 \times 10^5 . m^{-2}$ observed in 1970 and 1972 as compared with $30 \times 10^5 . m^{-2}$ in 1967 and 1982.

The increase in abundance was due principally to increases in C. b. thomasi. It was hypothesized that salmonid predation on planktivorous fish in the metalimnion had created a more favourable environment, particularly for C. b. thomasi, but that predator-prey relationships within the epilimnion had not changed significantly over the period compared, 1967-1982.

Because of sampling differences and site locations, exact comparisons of the highly heterogeneous benthic communities cannot be made with that of earlier surveys in Lake Ontario. Communities in the profundal zone of Lake Ontario remain as they were in the 1960s and will only change should the hypolimnion suffer oxygen depletion, or the phytoplankton biomass change dramatically. Population size at the deep station 41 was nearly constant over the sample period 1981 to 1983.

Beyond a depth of 20 m, generation times of the benthic community average one to two years. Therefore, seasonal fluctuations are a result of reproductive periods and changes in mortality rates of the populations. All the sites examined had no significant temporal variation in total biomass, with no spatial variation between the eastern and western sites in spite of the much greater depth at the Niagara site 93A. However, phytoplankton production was lower at 93A than at the eastern station 81. The increased organic loading from the Niagara River plume may be responsible for the higher than expected benthic abundance. The influence of the plume was also noted in the displacement of Gammarus and Physa offshore to depths of 50 m, as well as in thick deposition zone of organic debris, a large portion of which is terrestrial vegetation, eastward from the Niagara River at a depth of 30 to 50 m. Off station

93, between 30 and 50 m, Pontoporeia is absent, replaced by a large population of tubificids worms (7030 m^{-2}). These conditions have existed since the late 1960s (Kinney, 1972) and extend part way along the south shore to Rochester.

A comparison of integrated, two to three point discrete depth weighted average and 1 m samples of POC, PON, and CHLA indicated that discrete depth samples did not reliably describe epilimnion conditions. Integrated samples are recommended for all physical (except dissolved oxygen), nutrient, and biological measures. Integrated samples are also cheaper to analyze, faster to collect, and more appropriate for long-term monitoring.

Seasonally weighted mean concentrations and seasonal patterns were sensitive to sampling frequency. The physical parameters were the least sensitive, changing by less than $\pm$10 percent with "monthly" (four weeks) as compared with weekly sampling. Most nutrients were intermediate in sensitivity to sampling frequency, changing by $\pm$11 to 20 percent. The biological variables and SRP and NH_3 were extremely variable, changing by $\pm$27 to 34 percent (POC, PON, CHLA) or $\pm$42 to 64 percent (SRP, NH_3) with "monthly" sampling. Clearly, the biological and some nutrient variables need to be sampled at least weekly to obtain reasonably accurate estimates of seasonal patterns and annual means. Weekly sampling is sufficient to follow changes in the phytoplankton and zooplankton communities, and is recommended as the sampling interval for the program. Since the program tries to correlate the physical, nutrient, and biological parameters, the same sampling frequency should be adopted for all measures.

Station 93, located on the south shore, should be dropped from the program. It is very shallow (17.5 m) and subject to frequent physical changes and perturbations. These increased the variability and decreased the continuity and interpretability of the biological data.

Overall, the sampling regime and methods are appropriate and efficient for long term monitoring. Improvements should be made in the zooplankton sampling to account for species-specific vertical migrations and deep distributions during isothermal conditions. Zooplankton net efficiency should be assessed, and the importance of the other major biota (ciliates, rotifers, mysids) to energy transfer in the system should be investigated and their relevance to long term monitoring considered.

In conclusion, the program has proven very successful. By examining changes in the phytoplankton, zooplankton, and fish communities between the early 1970s and early 1980s, evidence was found suggesting a slight change in the trophic condition of the lake, but not in the overall functioning of the ecosystem. Salmonid predation may be influencing C. b. thomasi abundance, and therefore the ratio of copepods to cladocerans. However, there is no evidence that salmonids have had a significant impact on the alewife population and consequent functioning of the epilimnetic portion of the ecosystem.

The program has also been successful in describing seasonal patterns and normal annual variability of both physico-chemical measures and biological communities. As such, it has started a solid base for long term monitoring of the structure and functioning of Lake Ontario.

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REFERENCES

ANKAR, S. 1977. The soft bottom ecosystem of the northern Baltic proper with special reference to the macrofauna. Contrib. Asko Lab. Univ. Stockholm. No. 19: 1-48.

ANTON, A. AND H.C. DUTHIE. 1981. Use of cluster analysis in the systematics of the algal genus Cryptomonas. Can. J. Bot. 59:992-1002.

BOESCH, D.F. AND R. ROSENBERG. 1981. Responses to stress in marine benthic communities. In: G.W. Barrett and R. Rosenberg [Eds.]. Stress Effects on Natural Ecosystems:179-200. John Wiley and Sons Ltd.

BORGMANN, U., H. SHEAR, AND J.E. MOORE. 1984. Zooplankton and potential fish predation in Lake Ontario. Can. J. Fish. Aquat. Sci. 41:1303-1309.

BOYCE, F.M. 1974. Some aspects of Great Lakes physics of importance to biological and chemical processes. J. Fish. Res. Bd Can. 31: 689-730.

BRANDT, S.B., J.J. MAGNUSON, AND L.B. CROWDER. 1980. Thermal habitat partitioning by fishes in Lake Michigan. Can. J. Fish. Aquat. Sci. 37:1557-1564.

BRINKHURST, R.O., A.L. HAMILTON AND H.B. HERRINGTON. 1968. Components of the bottom fauna of the St. Lawrence Great Lakes. Univ. Toronto, Great Lakes Inst. No. PR 33: 1-49.

BROOKS, J.L. 1969. Eutrophication and changes in the composition of the zooplankton. In: Eutrophication: Causes, Consequences, Correctives. Proceedings of a Symposium:236-255. U.S. Nat. Acad. Sci.

BROOKS, J.L. AND S.I. DODSON. 1965. Predation, body size, and the composition of plankton. Science 150:28-35.

CARTER, J.C.H. 1969. Life cycles of Limnocalanus macrurus and Senecella calanoides, and seasonal abundance and vertical distributions of various planktonic copepods, in Parry Sound, Georgian Bay. J. Fish. Res. Bd. Can., 26:2543-2560.

CEDERWALL, H. 1976. Annual production of a soft bottom in the northern Baltic proper. In: B.F. Keegan (Ed.). Biology of Benthic Organisms:155-164. Pergamon Press.

CHRISTIE, W.J. 1974. Changes in the fish species composition of the Great Lakes. J. Fish. Res. Bd. Can. 31:827-854.

COOLEY, J.M., J.E. MOORE, AND W.T. GEILING. 1986. Population dynamics, biomass and production of the macro-zooplankton in the Bay of Quinte during changes in phosphorous loadings. Can. Spec. Publ. Fish. Aquat. Sci. (In Press).

CROWDER, L.B. AND J.J. MAGNUSON. 1982. Thermal habitat shifts by fishes at the thermocline in Lake Michigan. Can. J. Fish. Aquat. Sci. 39:1046-1050.

CZAIDA, S.C. 1974. Crustacean zooplankton of southwestern Lake Ontario in 1972 during the International Field Year for the Great Lakes. Internat. Assoc. Great Lakes Res. Proc. 17th Conf. Great Lakes Res. 1974:1-16.

CZAIDA, S.C. 1978. Crustacean zooplankton of southwestern Lake Ontario in spring 1973 and at the Niagara and Genesee Rivermouth areas in 1972 and spring 1973. J. Great Lakes Res. 4:1-9.

DADSWELL, M.J. 1974. Distribution, ecology and post-glacial dispersal of certain crustaceans and fishes in eastern North America. Nat. Mus. Can., Publ. Zool. No. 11. 110pp.

DILLON, P.J., K.H. NICHOLLS, AND G.W. ROBINSON. 1978. Phosphorus removal at Gravenhurst Bay. An 8 year study on water quality changes. Verh. Internat. Verein. Limnol. 20:263-277.

DUTHIE, H.C. AND M.R. SREENIVASA. 1971. Evidence for the eutrophication of Lake Ontario from the sedimentary diatom succession. Internat. Assoc. Great Lakes Res. Proc. 14th Conf. Great Lakes Res. 1971:1-13.

EL-SHAARAWI, A.H. AND R.E. KWIATKOWSKI. 1977. A model to describe the inherent spatial and temporal variability of parameters in Lake Ontario 1974. J. Great Lakes Res. 3:177-183.

FINDLAY, D.L. AND H.J. KLING. 1979. A species list and pictorial reference to the phytoplankton of Central and Northern Canada. Parts I and II . Can. Dept. Fish. Oceans, MS Rept. 1503.

FLANNAGAN, J.F. 1979. Efficiencies of various grabs and cores in sampling freshwater benthos. J. Fish. Res. Bd. Can., 27: 1691-1700.

FRICKER, H.J. AND A. ABBOTT. 1984. Zooplankton abundance in a north-south cross section of Lake Ontario (1982). Can. Dept. Environm., Nat. Wat. Res. Inst., Aquat. Ecol. Div. 99pp.

GLOOSCHENKO, W.A., J.E. MOORE, AND R.A. VOLLENWEIDER. 1972. The seasonal cycle of pheopigments in Lake Ontario with particular emphasis on the role of zooplankton grazing. Limnol. Oceanogr. 17(4):597-605.

GOLINI, V.I. 1979. Benthic macro- and meioinvertebrates of Lake Ontario, 1977: Distribution and relative abundance. Can. Dept. Fish. Environm., Fish. Mar. Serv., MS Rept. 1519. 41pp.

GREAT LAKES WATER QUALITY BOARD. 1983. 1983 Report on Great Lakes Water Quality: Report to the International Joint Commission, 130pp.

GRUMBLATT, J.L. 1976. IFYGL - An unusually cold year. IFYGL Bull. 18: 59-62.

HAWORTH, A.Y, AND H.G. BARBER. 1981. A guide to the morphology of the diatom frustule. Freshw. Biol. Assoc., Sci. Publ. No. 44.

HILTUNEN, J.K. 1969. The benthic macrofauna of Lake Ontario. Techn. Rep. Great Lakes Fish. Comm. 14: 39-50.

HORN, H. 1984. The effects of sampling intervals on phytoplankton growth and loss values derived from seasonal phytoplankton biomass variations in an artificial lake. Internat. Rev. ges. Hydrobiol. 69:111-119.

HOWMILLER, R.P. 1974. Composition of the oligochaete fauna of central Lake Michigan. Internat. Assoc. Great Lakes Res. Proc. 17th Conf. Great Lakes Res. 1974:589-592.

HUSTEDT, F. 1930. Bacillariophyta (diatomeae) In: A. Pascher, Die Susswasser - Flora Mitteleuropas Part I, 466pp. Jena, G. Fischer.

INLAND WATERS DIRECTORATE. 1979. Analytical Methods Manual. Can. Dept. Environm., Inl. Wat. Direct., Wat. Qual. Br. Ottawa.

JOHANNSSON, ORA E., R.M. DERMOTT, R. FELDKAMP AND J.E. MOORE. 1985. Lake Ontario Long Term Biological Monitoring Program: 1981, 1982 data base. Can. Data Rept. Fish. Aquat. Sci. 552.

JOHANNSSON, ORA E. AND C. K. MINNS. 1986. Examination of association indices and formulation of a composite seasonal dissimilarity index (in prep.).

JOHNSON, M.G. AND R.O. BRINKHURST. 1971. Production of benthic macroinvertebrates of Bay of Quinte and Lake Ontario. J. Fish. Res. Bd. Can. 28: 1699-1714.

KINNEY, W.L. 1972. The macrobenthos of Lake Ontario. Internat. Assoc. Great Lakes Res., Proc. 15th Conf. Great Lakes Res. 1972: 53-79.

KOLENOSKY, D. P. AND G. C. LETENDRE. 1984. Lake Ontario salmonid stocking and marketing program. Great Lakes Fish. Comm. 1984 Lake Ontario Comm. Rept.:181-212.

KRUEGER, C.C. and F.B. MARTIN. 1980. Computation of confidence intervals for the size-frequency (Hynes) method of estimating secondary production. Limnol. Oceanogr. 25: 773-777.

LANE, P.A. 1978. Role of invertebrates in structuring zooplankton communities. Verh. Internat. Verein. Limnol. 20:480-485.

LANE, P.A. 1979. Vertebrate and invertebrate predation intensity on freshwater zooplankton communities. Nature, 280:391-393.

LEHMAN, J.T., D.B. BOTKIN AND G.E. LIKENS. 1975. The assumptions and rationales of a computer model of phytoplankton population dynamics. Limnol. Oceanogr. 20:343-363.

LICHORAT, R.M. 1982. Summer distribution of salmonids in eastern Lake Erie. Ms D. Thesis. State University College, Fredonia, New York, U.S.A. 52pp.

LIN, C.K. AND C.L. SCHELSKE. 1978. Effects of nutrient enrichment, light and temperature on growth of phytoplankton from Lake Huron. Univ. Michigan, Great Lakes Res. Div., Spec. Rept. No.63.

LIND, E.M. AND A.J. BROOK. 1980. Desmids of the English Lake District. Freshw. Biol. Assoc. Sci. Publ. No.42.

LUND, J.W.G., C. KIPLING, AND E.D. LECREN. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimation of counting. Hydrobiologia 11:143-170.

LYNCH, M. 1979. The evolution of cladoceran life histories. Quart. Rev. Biol. 55:23-42.

MCNAUGHT, D.C. 1966. Depth control by planktonic cladocerans in Lake Michigan. Univ. Michigan, Great Lakes Res. Div., Pub. No.15:98-108.

MCNAUGHT, D.C., M. BUZZARD, AND S. LEVINE. 1975. Zooplankton production in Lake Ontario as influenced by environmental perturbations. U.S. Environm. Protect. Agency, Off. Res. Developm., Environm. Res. Center, Cornvallis, Oregon, 156pp.

MICHALSKI, M.F.P. 1968. Phytoplankton levels in Canadian near-shore waters of the Lower Great Lakes. Internat. Assoc. Great Lakes Res. Proc. 11th Conf. Great Lakes Res. 1968:85-95.

MINNS, C. K. 1984. Spatial and temporal variability in zooplankton abundance of the Great Lakes. Can. MS Rep. Fish. Aquat. Sci., 1750.

MUNAWAR, M. AND I.F. MUNAWAR. 1980. The importance of using standard techniques in the surveillance of phytoplankton indicator species for the establishment of long range trends in the Great Lakes: A preliminary example, Lake Erie. Can. Tech. Rep. Fish. Aquat. Sci. 976:59-86.

MUNAWAR, M. AND I.F. MUNAWAR. 1981. A general comparison of the taxonomic composition and size analysis of the phytoplankton of the North American Great Lakes. Verh. Internat. Verein. Limnol. 21:1695-1716.

MUNAWAR, M., I.F. MUNAWAR, P.E. ROSS AND A. DUGENAIS. 1982. Microscopic evidence of phytoplankton passing through glass-fibre filters and its implications for chlorophyll analysis. Arch. Hydrobiol. 94:520-528.

MUNAWAR, M. AND A. NAUWERCK. 1971. The composition and horizontal distribution of phytoplankton in Lake Ontario during the year 1970. Internat. Assoc. Great Lakes Res., Proc. 14th Conf. Great Lakes Res. 1971:69-78.

MUNAWAR, M., P. STADELMANN, AND I.F. MUNAWAR. 1974. Phytoplankton biomass, species composition and primary production at a nearshore and a mid-lake station of Lake Ontario during I.F.Y.G.L. Internat. Assoc. Great Lakes Res., Proc. 17th Conf. Great Lakes Res. 1974:629-652.

NALEPA, T.F. AND N.A. THOMAS. 1976. Distribution of macrobenthic species in Lake Ontario in relation to sources of pollution and sediment parameters. J. Great Lakes Res. 2: 150-163.

NALEWAJKO, C. 1966. Composition of phytoplankton in surface waters of Lake Ontario. J. Fish. Res. Bd. Can., 23:1715-1725.

NALEWAJKO, C. 1967. Phytoplankton distribution in Lake Ontario. Internat. Assoc. Great Lakes Res., Proc. Tenth Conf. Great Lakes Res. 1967:63-69.

NICHOLLS, K.H. 1981. Recent changes in the phytoplankton of Lakes Erie and Ontario. In: R.K. Cap and V.R. Frederick, [Eds]. Proceedings of the Conference on Changes in the Biota of Lakes Erie and Ontario. Bull. Buffalo Soc. Nat. Sci. 25:41-107.

NICHOLLS, K.H., L. HEINTSCH, E. CARNEY, J. BEAVER AND D. MIDDLETON. 1986. Some effects of phosphorus loading reductions on phytoplankton in the Bay of Quinte (Lake Ontario). Can. J. Fish. Aquat. Sci. (In Press).

NICHOLLS, K.H., D.W. STANDEN, AND G.J. HOPKINS. 1980. Recent changes in the near-shore phytoplankton of Lake Erie's western basin at Kingsville, Ontario. J. Great Lakes Res. 6(2):146-153.

NYGAARD, G. 1977. New or interesting plankton algae. Det Kongelige Danske Videnskabernes Selskab Biologisk Skrifter 21.

O'GORMAN, R., R. BERGSTEDT, AND C.P. SCHNEIDER. 1984. Status of major forage fish stocks in Lake Ontario. Ann. Meeting, Lake Ontario Committee. Great Lakes Fishery Commission. 1984: 49-53.

O'GORMAN, R. AND C.P. SCHNEIDER. 1986. Dynamics of alewives in Lake Ontario following a mass mortality. Trans. Amer. Fish. Soc. (In press).

OLSON, R.A. 1984. Summer resource utilization by salmonids and their prey in Lake Ontario. M.Sc. Thesis, State University College, Fredonia, N.Y., U.S.A.

PARKER, J.I. 1980. Predation by Mysis relicta on Pontoporeia hoyi: a food chain link of potential importance in the Great Lakes. J. Great Lakes Res. 6: 164-166.

PATALAS, K. 1969. Composition and horizontal distribution of crustacean plankton in Lake Ontario. J. Fish. Res. Bd. Can., 26:2135-2164.

PATALAS, K. 1972. Crustacean plankton and the eutrophication of St. Lawrence Great Lakes. J. Fish. Res. Bd. Can., 29:1451-1462.

PATRICK, R. AND C.W. REIMER. 1966. The diatoms of the United States - exclusive of Alaska and Hawaii Volume I. Monogr. Acad. Nat. Sci. Philadelphia, No. 13.

PATRICK, R. AND C.W. REIMER. 1975. The diatoms of the United States exclusive of Alaska and Hawaii Volume II, Part 1. Monogr. Acad. Nat. Sci. Philadelphia, No. 13.

PHILBERT, F.J. AND W.J. TRAVERSY. 1973. Methods of sample treatment and analysis of Great Lakes water and precipitation samples. Internat. Assoc. Great Lakes Res., Proc. 16th Conf. Great Lakes Res. 1973:294-308.

POWERS, C.F. and A. ROBERTSON. 1967. Design and evaluation of an all purpose benthic sampler. Univ. Michigan, Great Lakes Res. Div., Spec. Rept., 30:126-131.

PRESCOTT, G.W. 1970. Algae of the Western Great Lakes area. Wm. C. Brown Co. Publ., Dubuque, Iowa.

PRESCOTT, G.W., T.H. CROASDALE AND W.C. VINYARD. 1975. A synopsis of North American desmids Part II. Desmidiaceae Placodermae Section 1. University of Nebraska Press, Lincoln.

RAMBERG, L. 1979. Relations between phytoplankton and light climate in two Swedish forest lakes. Internat. Rev. ges. Hydrobiol. 64:749-782.

RAVERA, O. 1980. Effects of eutrophication on zooplankton. Progress Wat. Technol., 12:141-159.

REYNOLDS, C.S. 1984. The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge, U.K. 328pp.

RILEY, G.A. 1957. Phytoplankton of the north central Sargasso Sea, 1950-52. Limnol. Oceanogr. 2:252-270.

ROSA, F. 1985. Sedimentation and sediment resuspension in Lake Ontario. J. Great Lakes Res. 11:13-25.

SCAVIA, D. 1979. Examination of phosphorous cycling and control of phytoplankton dynamics in Lake Ontario with an ecological model. J. Fish. Res. Bd. Can. 36:1336-1346.

SCAVIA, D. AND J.R. BENNETT. 1980. Spring transition period in Lake Ontario - a numerical study of the causes of the large biological and chemical gradients. Can. J. Fish. Aquat. Sci. 37:823-833.

SCHELSKE, C.L., L.E. FELDT, M.A. SANTIAGO AND E.F. STOERMER. 1972. Nutrient enrichment and its effect on phytoplankton production and species composition in Lake Superior. Internat. Assoc. Great Lakes Res., Proc. 15th Conf. Great Lakes Res. 1972:149-165.

SCHELSKE, C.L. AND E.F. STOERMER. 1972. Phosphorous, silica, and eutrophication of Lake Michigan. In: G.E. Likens (Ed.), Nutrients and Eutrophication: The Limiting Nutrient Controversy. Vol. 1:157-171. Amer. Soc. Limnol. Oceanogr., Allen Press Inc., Lawrence, Kansas, U.S.A.

SCHOEMAN, F.R. AND R.E.M. ARCHIBALD. 1976-1979. The diatom flora of South Africa. SCIR Special Report WAT, Parts 1-1V.

SCOTT, W. B. AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Bd. Can. 184. 966pp.

SEIGFRIED, C.A. 1985. Life history, population dynamics and production of Pontoporeia hoyi (Crustacea, Amphipoda) in relation to the trophic gradient of Lake George, New York. Hydrobiologia 122: 175-180.

SIMONS, T.J. 1976. Analysis and simulation of spatial variations of physical and biochemical processes in Lake Ontario. J. Great Lakes Res. 2:215-233.

SMITH, G.M. 1950. The fresh-water algae of the United States. McGraw-Hill Book Co., New York.

SREENIVASA, M.R. AND C. NALEWAJKO. 1975. Phytoplankton biomass and species composition in northeastern Lake Ontario, April-November, 1965. J. Great Lakes Res. 1:151-161.

SRIDHARAN, N. AND G.F. LEE. 1977. Algal nutrient availability and limitation in Lake Ontario during IFYGL. Part III. U.S. Environm. Protect. Agency, EPA-600/3-77-046a.

STADELMANN, P., J.E. MOORE AND E. PICKETT. 1974. Primary production in relation to temperature structure, biomass concentration, and light conditions at an inshore and offshore station in Lake Ontario. J. Fish. Res. Bd. Can. 31:1215-1232.

STEVENS, R.J.J. AND M.A.T. NEILSON. 1986. Response of Lake Ontario to reductions in phosphorous load: 1967-1982. (in preparation).

STOERMER, E.F. AND J.J. YANG. 1969. Plankton diatom assemblages in Lake Michigan. Univ. Michigan, Great Lakes Res. Div., Spec. Rept., No. 47. 268pp.

STOERMER, E.F., M.M. BOWMAN, J.C. KINGSTON AND A.L. SCHAEDEL. 1975. Phytoplankton composition and abundance in Lake Ontario during I.F.Y.G.L. U.S. Environm. Protect. Agency, EPA-660 13-75-004.

STOERMER, E.F., AND T.B. LADEWSKI. 1984. Phytoplankton associations in Lake Ontario during IFYGL. Univ. Michigan, Great Lakes Res. Div., Spec. Rept., No. 62. 106pp.

STRICKLAND, J.D.H. AND T.R. PARSONS. 1968. A practical handbook for seawater analysis. Bull. Fish. Res. Bd. Can. No.167.

TAFT, C.E. AND C.W. TAFT. 1971. The algae of Western Lake Erie. Bull. Ohio Biol. Surv. 3:1-189.

TILMAN, D. 1981. Tests of resource competition theory using four species of Lake Michigan algae. Ecology 62:802-815.

TORKE, B.G. 1975. The Population Dynamics and Life Histories of Crustacean Zooplankton at a Deep Water Station in Lake Michigan. Ph.D. Thesis. University of Wisconsin-Madison. Madison, Wisconsin. U.S.A. 91pp.

UTERMÖHL, H. 1958. Zur Vervolkommung der quantitative Phytoplankton. Method. Mitt. Internat. Verein. Limnol. 9:1-38.

VOLLENWEIDER, R.A. 1968. Scientific Fundamentals of the Eutrophication of Lakes and Flowing Waters, with Particular Reference to Nitrogen and Phosphorous as Factors in Eutrophication. Organization for Economic Co-operation and Development, Paris. 159pp.

VOLLENWEIDER, R.A., M. MUNAWAR, AND P. STADELMANN. 1974. A comparative review of phytoplankton and primary production in the Laurentian Great Lakes. J. Fish. Res. Bd. Can. 31:739-762.

WATSON, N.H.F. AND G.F. CARPENTER. 1974. Seasonal abundance of crustacean zooplankton and net plankton biomass of Lakes Huron, Erie, and Ontario. J. Fish. Res. Bd. Can. 31:309-317.

WEBBER, C.I. 1971. A guide to the common diatoms at water pollution surveillance system stations. U.S. Environm. Protect. Agency, Nat. Environm. Res. Center, Analyt. Qual. Control Lab., Cincinnati, Ohio, U.S.A.

WELLS, L. 1960. Seasonal abundance and vertical movements of planktonic crustacea in Lake Michigan. U.S. Fish Wildl. Serv., Fish. Bull., 60:343-369.

WELLS, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnol. Oceanogr. 15:556-565.

WETZEL, R.G. 1975. Limnology. W.B. Saunders Company. Toronto. 743pp.

WILSON, J.B. AND J.C. ROFF. 1973. Seasonal vertical distributions and diurnal migration patterns of Lake Ontario crustacean zooplankton. Internat. Assoc. Great Lakes Res., Proc. 16th Conf. Great Lakes Res. 1973:190-203.